An investigation into declining skink populations and their behavioural responses to introduced mammalian predators

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Abstract

New Zealand provides an excellent example of the effect of exotic predators on native reptile populations. Prior to human arrival, reptiles evolved in the absence of mammalian predators but are now sympatric with 11 introduced mammalian predators. New Zealand's reptile populations have declined over the past millennium because they have few defensive behaviours against this new predator guild. However, relatively few studies have investigated the effects of introduced mammalian predators on skinks. In this thesis, I studied the life history of several skink species and the long-term demographic changes in these species to evaluate population trends. I evaluated the effectiveness of mammalian predator control in the Rotoiti Nature Recovery Project (RNRP) for restoring skink populations and I investigated the potential sub-lethal effects of mammalian predators on skinks. Finally, I tested whether two skink species had developed behaviours to avoid the scent of introduced rats or hedgehogs. I estimated size at sexual maturity, birthing season and habitat preferences for speckled skinks (*Oligosoma infrapunctatum*) in the Nelson Lakes area. My research shows that skink populations are declining both inside and outside of the RNRP. The largest declines are seen in the rarer species and even within the predator-controlled area of the RNRP the speckled skink is nearing extirpation. In addition, the proportion of female northern grass skinks (*O. polychroma*) and larger individuals of both sexes has decreased since 1970; suggesting females and larger individuals are more vulnerable to predation. An investigation of three fitness surrogates (body condition, parasite load and prevalence of caudal autotomy) showed that for both northern grass and glossy brown skinks (*O. zelandicum*), body condition was significantly lower in populations with mammalian predators than without. This has serious conservation implications because it shows that lizard populations may not only be in decline from direct predation, but also additional stresses associated with predation that may lead to reduced reproductive output. Neither parasite load, nor the prevalence of caudal autotomy, appears to be good indicators of fitness for northern grass or glossy brown skinks. I found no evidence of substantial avoidance behaviours in glossy brown and northern grass skinks to either rat or hedgehog odour. Two hypotheses are suggested to explain this. Firstly, there may not have been enough time for these species to evolve avoidance behaviours, and secondly, there may be insufficient selection pressure due to the high efficiency of the alien predators, or because rats and hedgehogs are active foragers and thus scent gives the prey limited

information on immediate predation pressure. This lack of evidence for the evolution of anti-predator behaviour, in addition to reduced body condition and population decline in areas with mammalian predators present, highlights the importance of intensive mammalian predator control for the continued survival of skink species on mainland New Zealand.

Chapter 1: General Introduction

Effects of invasive predators on reptiles

When humans colonise new areas they bring with them exotic organisms, of which many become pests (Atkinson, 1989). Introduced species may soon surpass habitat loss as the main cause of global environmental degradation (Chapin III et al., 2000). As native species have not coevolved with the introduced competitors and predators that they now encounter, biotic interactions can be expected to be severe (Case and Bolger, 1991; Salo et al., 2007). A meta-analysis shows that some exotic predators can have double the impact of native predators on prey populations (Salo et al., 2007). This is because the evolutionary 'arms race' that exists between predators and prey in ecosystems in which they co-evolved (Dawkins and Krebs, 1979; Endler, 1986; Van Valen, 1973) breaks down when either predators or prey are introduced into or removed from a system (Coss, 1999; Strauss et al., 2006). In addition, when prey is not the primary food of a predator, such as in the relationship between introduced predators and endemic prey species, predator-prey theory predicts that the effects of predation are inversely dependant (Salo et al., 2007). This can lead to a decline in the native fauna without a concomitant decline in the introduced predator (Salo et al., 2007).

Reptile species are declining globally, with invasive species being identified as one of the five main causes, along with habitat loss and degradation, environmental pollution, global climate change and unsustainable use (Gibbon et al., 2000). Reptiles have integral value to natural ecosystems, making their disappearance a concern (Gibbons and Stangel, 1999). There are many examples of reptile populations being negatively affected by introduced predators. In the continental United States, introduced fire ants (*Solenopsis invicta*) were found to prey on both the eggs (Moulis, 1997) and young (Allen et al., 1997) of turtles and alligators, and it has been proposed that they are the primary cause of extirpation of the Texas horned lizard (*Phrynosoma cornutum*) from part of its range (Goin, 1992). In Australia, predation by introduced mammalian predators, including foxes (*Vulpes vulpes*) and feral cats (*Felis domesticus*), was ranked the

fourth highest threat to reptile populations, after three types of habitat destruction (Cogger et al., 1993).

Invasive species are considered to be the primary cause of extinctions in island ecosystems (Clout and Veitch, 2002). The arrival of humans on islands is closely linked to increased extinction rates of reptiles (Case et al., 1998; Pregill, 1986). This is thought to be due to predation by introduced species in conjunction with habitat destruction (Case et al., 1998; Pregill, 1986). In island ecosystems, 'relaxed selection' often occurs in regard to anti-predator behaviours as whole classes of predators can be absent from a system. For example, New Zealand did not have any mammalian predators until the arrival of humans (Worthy and Holdaway, 2002). In such a system, there is no selection pressure to maintain or evolve anti-predator adaptations for the class of predator that is not present, and thus these traits are lost (Coss, 1999), especially if they are costly to maintain (Blumstein and Daniel, 2005; Coss, 1999). In a synthesis of the effects of introductions on the abundance and distribution of insular reptiles, Case and Bolger (1991) found that introduced predators caused extinctions and severe reductions in the abundance of both native and introduced reptiles, but with the greatest negative effects on 'predator-naive' native species. Islands without introduced predators tend to have higher densities and diversity of reptile species than their counterparts with invasive predators (Case and Bolger, 1991). As a result, predation has been considered the main cause of most reptile extinctions and declines on islands, as opposed to other biotic variables such as pathogens and competitors that may vary with island size (Case and Bolger, 1991). The negative effect of invasive predators such as rats (*Rattus rattus* and *R. norvegicus*), housecats, dogs (*Canis familiaris*), Indian mongoose (*Herpestes auropunctatus*) and snakes has been well recorded (Case and Bolger, 1991).

Different species of invasive predators can have differing effects on native reptiles, but as rats are partially arboreal they affect a larger range of reptile species than non-arboreal predators (Case and Bolger, 1991). The arrival of rats on islands is correlated with a rapid decline in the density and diversity of lizards (McCallum, 1986; Towns and Daugherty, 1994). Islands without rats can have up to 20 fold higher densities of lizards than islands with rats, as well as a higher diversity of species (Parrish and Pierce, 1993; Towns, 1991; Whitaker, 1973, 1978). For

example, when kiore/Pacific rat (*R. exulans*) colonised an island in the Mokohinau Group (New Zealand) they caused a dramatic decrease in lizard abundance (McCallum, 1986). After the removal of the rats the lizard abundance increased, although by that stage two species had become locally extinct (McCallum, 1986). Likewise, when Norway rats invaded Whenuakura Island, New Zealand, in 1983 and 1984, within one year tuatara (*Sphenodon punctatus*) which were previously abundant, had become locally extinct, as had nearly all the lizards (Newman, 1986). Rats are thought to have caused extinctions of multiple lizard species on islands throughout the world, including the Canary Islands, the Cape Verde Islands, Norfolk Island and Lord Howe Island (Case and Bolger, 1991).

Domestic cats (and feral populations of domestic cats) have also been associated with the extinction of reptiles on islands. Large, tame lizard species seem to be especially vulnerable to cat predation. For example, in the Mascarene Islands two large gecko species became extinct following the introduction of cats (Vinson and Vinson, 1969). In the Canary Islands, cats caused decreases in the populations of three giant lizard species, especially the La Gomera giant lizard (*Gallotia gomerana*) (Nogales et al., 2006). In this island group, reptiles made up a substantial part of the diet of feral cats (Nogales, 1996). On the Mascarenes Islands, two large geckos in the genus *Phelsuma* became extinct after rats and cats were introduced (Vinson, 1969). In Fiji, the arboreal lizards, including the now rare endemic Fijian iguanas (*Brachylophus* sp.), have been strongly affected by cat predation, potentially even to a greater extent than from that of the introduced mongoose (Gibbons and Watkins, 1982). Substantial populations of iguanas are now only found on small islands lacking both of these mammals (Gibbons and Watkins, 1982). Similarly, the large iguanine *Cyclura carinata* was reduced from about 5500 individuals to just five individuals on Pine Cay (Caicos Islands) during the construction of a hotel and tourist area that resulted in the introduction of dogs and cats (Iverson, 1978). The decline of this species is mirrored elsewhere in the Turks and Caicos Islands due to the introduction of these mammals (Iverson, 1978).

Similar to the effects of introduced mammalian predators, the introduction of the brown tree snake (*Boiga irregularis*) is thought to be the main cause of the extinction of the gecko *Nactus pelagicus* from the islands of Guam and Tinian, as well as causing dramatic declines in multiple species of lizard on 13 of the Marianas Islands (Rodda, 1992). In contrast and unlike native

reptiles, introduced reptiles on islands are, in general, not as strongly affected by the presence of introduced predators, of any guild (Case and Bolger, 1991). This is probably due to the fact that nearly all introduced reptile species come from predator-rich continental areas, and as a result possess adaptations to withstand these predators (Case and Bolger, 1991). For example, the introduced Australian rainbow skink (*Lampropholis delicata*) has more anti-predator behaviours towards mammalian predators than the native northern grass skink (*Oligosoma polychroma*) (Hoare, 2006a). The presence of predators may even enhance the success of introduced reptile species because they may moderate competition with natives (Case and Bolger, 1991).

The effect of introduced mammalian predators on New Zealand reptiles

New Zealand has one of the most diverse endemic reptile assemblages of any temperate archipelago (Daugherty et al., 1990). At least 109 species of lizard (Hitchmough et al., 2010) and the only species of tuatara (Hay et al., 2010) occur in New Zealand. All three genera of New Zealand geckos are endemic and considered some of the world's most primitive (Kluge, 1967), and may be Gondwanan relics (Chambers et al., 2001). New Zealand's skinks are considered to comprise only one genera and thought to have colonised the islands via long-distance overwater dispersal from New Caledonia in the early Miocene (16–22.6 mya) (Chapple et al., 2009).

Prior to human arrival it is thought that New Zealand hosted not only a higher diversity of species, but also higher densities of reptiles than currently found anywhere on the main islands. On predator-free offshore islands lizard numbers can still be extraordinarily high, with estimates of up to 1390 individuals per acre (Crook, 1973; Whitaker, 1968, 1973). Since the arrival of humans, New Zealand has lost three species of lizard (Bauer and Russell, 1986; Hardy, 1977; Worthy, 1987a) and many of the extant species have drastically reduced populations (Bull and Whitaker, 1975; Daugherty et al., 1994; Hitchmough et al., 2013; Towns and Daugherty, 1994; Worthy, 1987c). Tuatara (Bull and Whitaker, 1975) and 37% of New Zealand's lizard species (Towns et al., 2001) are currently restricted to offshore islands without mammalian predators, expect for a few reintroductions to mammal free 'mainland islands'. There is strong evidence that all but two lizard species (Grigg et al., 1985) once had much larger distributions on the main islands (Bull and Whitaker, 1975; Cassels, 1984; Towns and Daugherty, 1994; Worthy, 1987c),

with no known range contractions prior to human arrival (Towns and Daugherty, 1994). Under the New Zealand Threat Classification System List of endemic species, 32 species of reptiles are threatened and 50 species of reptiles are considered at risk (Hitchmough et al., 2013). Twenty nine species are also listed as threatened globally (IUCN, 2015).

The main hypotheses for the observed range contractions and extinctions of reptiles in New Zealand are predation by introduced mammals (Worthy and Holdaway, 2002), and habitat destruction (Towns and Daugherty, 1994). New Zealand provides an excellent example of the effect of exotic predators on native reptile populations. Prior to human contact 1250-1300 years ago (Anderson, 1991; Wilmshurst and Higham, 2004), there were no terrestrial mammals present since the Middle Miocene (16 – 11.5 Ma) (Worthy et al., 2006), except for three species of bat (Anderson, 1996; Holdaway, 1996; Worthy and Holdaway, 2002). Since then 11 mammalian predators have been introduced (Table 1.1); this is more than any other archipelago (Towns et al., 1997).When Māori arrived in New Zealand they brought with them kiore, and the dog (*Canis familiaris*) (Table 1.1). With the arrival of Europeans, more mammalian predators were introduced between 1790 and 1886 (Table 1.1). All these species are known to eat lizards (Bettesworth, 1972; Bettesworth and Anderson, 1972; Cuthbert et al., 2000; Daugherty and Towns, 1991; Jones et al., 2005; King, 2005; Newman, 1994; Newman and McFadden, 1990; Norbury, 2001; Worthy and Holdaway, 2002). Reptile extinctions (localised and complete) occurred in waves that followed each of the predator introductions (Towns and Daugherty, 1994). The extinction of the lizards *Oligosoma alani* and *C. macgregori* (Towns and Daugherty, 1994) as well as tuatara (Cree et al., 1995) from the mainland are attributed to the introduction of the kiore. They represent the first wave of reptile extinctions (Towns and Daugherty, 1994). Norway rats are more detrimental to reptiles than kiore (Newman, 1986). The combined effect of the two rat species probably lead to a second wave of extinctions on the mainland, including species such as Duvaucel's gecko (Towns and Daugherty, 1994). The third wave of extinctions occurred with the introduction of arboreal ship rats, cats and mustelids, as they could reach both arboreal and terrestrial species (Towns and Daugherty, 1994).

In addition to predation, mammalian predators may compete with some species of reptiles for food (Tyrrell et al., 2000) as invertebrates and soft fruits are an important food source for both

rodents (Best, 1969; Bettesworth, 1972; Daniel, 1973) and lizards (Whitaker, 1978). Kiore has been implicated in the local extinction and decline of many invertebrates that are an important food sources to lizards (Atkinson and Moller, 1990; Towns, 2009). In addition, rats can suppress honeydew, which is a substantial food source for some geckos (Towns, 2002).

Although the New Zealand reptile fauna appears especially vulnerable to introduced mammalian predators, they did experience predation, though from a very different predator guild. New Zealand reptiles co-evolved with a suite of avian (Oliver, 1955) and reptilian predators, which are largely visually-oriented and thus they evolved anti-predator strategies such as cryptic coloration and secretive behaviour which reduced detection (Worthy and Holdaway, 2002). These behaviours are potentially not effective anti-predation strategies against rats, hedgehogs and other predators as they hunt primarily using olfactory cues (Armsworth et al., 2005; King, 2005). Furthermore, due to relaxed selection against mammalian predators, traits such as gigantism (Bauer and Russell, 1986), ground foraging behaviour and K-selected life history strategies, including vivipary (Robb, 1986), evolved in New Zealand reptiles (Cree, 1994; Wilson, 2004). These traits make them highly vulnerable to predation by introduced mammals (Atkinson, 1989; Cree, 1994; Newman and Watson, 1985). Nocturnal, terrestrial, and large species of New Zealand reptiles that forage in the open are especially at risk from mammalian predation (Whitaker, 1978) as the majority of the introduced mammalian predators are nocturnal (King, 2005). Prior to rats being removed from Korapuki Island, there were significantly fewer nocturnal than diurnal species of reptiles compared to neighbouring rat-free Middle Island (Towns, 1991). Terrestrial species are more vulnerable as most mammalian predators are terrestrial (King, 2005). Small species also appear less vulnerable to predation than large ones, probably due to being able to hide in spaces too small for larger predators to access (Whitaker, 1978). The largest extant gecko, Duvaucel's gecko (*Hoplodactylus duvaucelii*), is restricted to offshore islands free of mammalian predators. The same is true for the four largest extant skinks, except for one small vulnerable population on the mainland (Hoare et al., 2007a). All these species appear to have formerly been widespread (Worthy, 1987b). Species which forage in the open are more vulnerable to predation perhaps because they are more easily found by predators (Whitaker, 1978). Species showing these characteristics, such as tuatara, are those with the most disjunct current distributions (Whitaker, 1978).

While it is well established that introduced mammalian predators are detrimental to indigenous lizard populations in New Zealand, there has been little work done on determining how much predator control is needed to restore lizard populations (Tocher, 2006), whether New Zealand lizards are developing any novel anti-predator strategies to mammalian predators (Hoare, 2006a; Hoare et al., 2007c; Towns et al., 2006), and whether mammalian predators are causing sub-lethal effects on lizards (Barr, 2009; Christmas, 1995). This thesis investigates these questions (Table 1.2) using four indigenous skink species.

Study species

Four species of skinks were studied: northern grass skink (*Oligosoma polychroma*), speckled skink (*O. infrapunctatum*), spotted skink (*O. lineoocellatum*) and glossy brown skink (*O. zelandicum*). All four species are all diurnal, give birth to live young and are indigenous to New Zealand (Whitaker, 2000).

Northern grass skink: The northern grass skink is found throughout central and eastern New Zealand (Jewell, 2011). It typically lives in densely-vegetated grassland or shrub-land from littorial to subalpine zones (Freeman, 1997; Whitaker, 2000). They are most active in the middle of the day (6-9 hrs after sunrise, Freeman, 1997). Northern grass skinks have been found to eat a wide range of invertebrates including Coleoptera, Araneae, Lepidoptera larvae, Orthoptera, Diptera, Hemiptera, and arthropod eggs (Freeman, 1997; Patterson, 1992; Spencer et al., 1998). However, they also eat fruits such as that from the native shrub *Leucopogon* sp. and the introduced blackberry (*Rubus fructicosus*) (Freeman, 1997; Patterson, 1992; Spencer et al., 1998). The northern grass skink species is composed of multiple distinct clades (Liggins et al., 2008). All northern grass skinks in this study are from clade 1b (Liggins et al., 2008), which is not considered threatened, though it is conservation dependant (Hitchmough et al., 2013).

Speckled skink: The speckled skink is found in the central North Island, and in the Nelson and Westland regions of the South Island (Whitaker, 2000). It is localised and rare within the Nelson/Marlborough Conservancy where it is found only on Stephens Island, and at isolated sites

at Golden Downs and in the upper Buller catchment (Whitaker, 2000). They typically inhabit densely vegetated grassland, shrub-land or fern-land below 900 m (Whitaker, 2000). The speckled skink is listed on the New Zealand Threat Classification List as at risk, due to having a sparse population in partial decline. Although its overall area of occupancy is more than 100,000 ha at present, it is predicted to decline 10-70% (Hitchmough et al., 2013). The speckled skink is also listed on the IUCN Red List as near threatened (IUCN, 2015).

Spotted skink: The spotted skink is found from Hawkes Bay to south Canterbury (Whitaker, 2000). It is widespread in Nelson and Marlborough east of the Waimea basin (Whitaker, 2000). It inhabits dry scrubby and rocky areas and subalpine grassland to at least 1600 m (Whitaker, 2000). Like the northern grass skink, the spotted skink species is composed of multiple clades (Greaves et al., 2007). All the spotted skinks in this study are from clade 1b (Greaves et al., 2007). This clade is considered to have a relict population, with more than 20,000 mature individuals and is stable or increasing (Hitchmough et al., 2013). However, these populations are sparse and some are in decline (Hitchmough et al., 2013).

Glossy brown skink: The glossy brown skink is found in the Marlborough Sounds as well as the western North Island and Wellington (Whitaker, 2000). They typically live in grasslands, shrub-lands and open forest (Whitaker, 2000). Food, in order of preference is thought to be: spiders, hemipterans, coleopterans, isopods, amphipods and fruits (Barwick, 1959). They have home ranges of about 15 m^2, but they do not appear to be territorial as home ranges overlap (Barwick, 1959). They reduce activity from mid April until the end of August, but is only partial, and individuals are known to become active in warm weather to bask and eat (Barwick, 1959). The glossy brown skink is listed as at risk on the New Zealand Threat Classification List due to being in partial decline with a total area of occupancy for over 100 km^2 with an expected to population decline of 10 -70% (Hitchmough et al., 2013). It is also on the IUCN Red List, categorised as of least concern (IUCN, 2015).

Outline of thesis

My thesis is comprised of four studies (Chapters 2 to 5), each of which investigates a different aspect of the relationship between introduced mammalian predators and native skinks (Table 1.2). Each chapter has been written in manuscript style (in preparation for publication) and can be read independently. However, as a result there is some necessary repetition.

In Chapter 2, I focus on increasing our understanding of the life history of the three extant skinks species in the Nelson Lakes area (northern grass, speckled and spotted skinks) through the use of a long term demographic survey. In addition I investigate the habitat preferences of speckled skinks, and whether this differs between sexes and size cohorts. I then compared my results to those from the same site in the 1970's (Spencer et al., 1998) to investigate whether the demographics have changed over time.

Next, I examine the usefulness of the mammalian predator control being conducted within the Rotoiti Nature Recovery Project (RNRP) for the recovery of indigenous skink populations (Chapter 3). I ask the question: are the indigenous skink populations increasing within the RNRP following mammalian predator control implemented in 2001? I address this question by reporting on a 10 year survey of skink populations using live capture pit-fall trapping at two sites within the RNRP. I also investigated whether skinks populations where undergoing a similar decline outside of the RNRP. To do this I conducted a two year pit-fall trapping study as Lake Station, which has a history of lizard research. Therefore, I was able to compare my findings to a similar study conducted in 1995 (Efford et al., unpubl. data) to determine whether the skink communities have changed since then.

Chapter 4 investigates whether introduced mammalian predators are causing sub-lethal predation effects on northern grass and brown skinks. I explore this by comparing three potential effects of sub-lethal predation: caudal autotomy, parasite load and body condition of skinks in populations with and without mammalian predators.

Finally, in Chapter 5 I test whether the glossy brown skink and northern grass skink have developed the ability to detect and avoid the faecal scent of two introduced mammalian predators

(ship rat and hedgehog). I used a lab study of behavioural responses to the experimental presentations of odours. Each skink was placed in a terrarium with a choice of two retreats, one with either a predator or control scent, and the other one scent-free. My objective was to determine whether a skink would avoid a retreat that contained the odour of an introduced predator, suggesting it has developed the ability to recognise and avoid novel threats.

In Chapters 4 and 5, I chose northern grass and glossy brown skinks as my study species because they are fairly common, thus increasing my ability to find multiple populations to compare and enough individuals to give statistical robustness. In both chapters I use Maud Island (Marlborough Sounds), Pukerua Bay (south western North Island) and Manaroa (mainland Marlborough Sounds) as study sites. Since Maud Island is one of the few locations in New Zealand that has never had mammalian predators present and hosts a large population of glossy brown skinks, it was chosen as my mammalian predator-free site for glossy brown skinks. Pukerua Bay is the closest known large population of glossy brown skinks to Maud Island, and thus was chosen as the mammalian predator-present site for this species. Given Manaroa's proximity to Maud Island and North Brother Island, it was used as the mammalian predator site for northern grass skinks. Due to the lack of avoidance of rats of hedgehogs in northern grass skinks from Manaroa (see Chapter 5) I did not repeat the study in an area without mammalian predators. In Chapter 4, I use data collected by Hoare (2006) from North Brother Island on the fitness characteristics of northern grass skinks as it is a mammalian predator-free area. In Chapter 4 I also use data collected during the field work conducted for Chapters 2 and 3 as an additional site with mammalian predators and northern grass skinks. I would have preferred to use sites that had both northern grass and glossy brown skinks present, but I was unable to find such areas.

Chapter 6 concludes this work with a synthesis of my findings on the effects of introduced mammalian predators on New Zealand skinks. I discuss the contribution of these findings to our understanding of how invasive predators influence naïve prey, and how effective current levels of predator control strategies are in protecting native lizards. I also suggest how these findings can improve present conservation measures, and identify directions for future research.

Tables

Table 1.1: Sequence of introductions of mammalian predators to New Zealand. Reported introduction dates may vary between the North and South Islands (King, 2005; Towns and Daugherty, 1994).

Species		**Date of introduction (A.D)**
Pacific rat/kiore	*Rattus exulans*	c. 1000
Dog	*Canis familiaris*	c. 1000
Pig	*Sus scrofa*	1790-1840
Norway rat	*Rattus norvegicus*	1790-1850
Mouse	*Mus musculus*	1830-1850
Cat	*Felis catus*	1830-1850
Possum	*Trichosurus vulpecula*	1858-1920
Ship rat	*Rattus rattus*	1860-1890
Ferret	*Mustela furo*	1879-1890
Weasel	*Mustela nivalis*	1885-1886
Stoat	*Mustela erminea*	1885-1886

Table 1.2: Summary of thesis research questions and how they were investigated.

Research Question	Investigation	Chapter
What are the life history traits of northern grass, spotted and speckled skinks in the St. Arnaud area?	Ten year demographic survey using live capture pit-fall traps of skink populations in the Nelson Lakes area within the Rotoiti Nature Recovery Project (RNRP), coupled with a two year survey at Lake Station to compare demographics to those in the 1970's (Spencer et al., 1998).	Chapter 2
Are the indigenous skink populations increasing within the RNRP in Nelson Lakes National Park following mammalian predator control implemented in 2001?	Ten year demographic survey of skink populations using live capture pit-fall trapping at two sites within the RNRP.	Chapter 3
Have the skink population demographics at Lake Station changed significantly since 1996?	Compared my two year demographic survey using live capture pit-fall traps with a similar study in 1995 (Efford et al., unpubl. data).	
Are introduced mammalian predators causing substantial sub-lethal fitness effects on indigenous skink populations?	I investigated three possible effects of sub-lethal predation: caudal autotomy, parasite load and body condition in northern grass and glossy brown skinks. Populations with and without the presence of introduced mammalian predators were compared.	Chapter 4
Do the indigenous New Zealand glossy brown and northern grass skink have the ability to detect and avoid the faecal scent of two introduced mammalian predators (ship rat and hedgehog)?	Behavioural study in which each skink was placed in a terrarium with a choice of two retreats, one with either a predator or control scent, and the other one scent-free. Skinks were filmed for 12 hours to record which retreats were entered and the duration of each visit.	Chapter 5

Chapter 2: Life history traits of speckled, northern grass and spotted skinks in the St. Arnaud area, New Zealand; with a focus on speckled skinks

Abstract

Three species of skink are known to reside in the Rotoiti Nature Recovery Area (RNRP) and the surrounding area of the South Island, New Zealand: the northern grass skink (*Oligosoma polychroma*), speckled skink (*O. infrapunctatum*) and spotted skink (*O. lineoocellatum*). As there has been limited research on the life history of these species, I used a live trapping study of each species to estimate sex ratio and measure body size. I estimated the size at sexual maturity, birthing season and habitat preferences for speckled skinks. I then compared my results with an earlier study of skinks at Lake Station, outside of the RNRP. Since the 1970's the proportion of female northern grass skinks caught at Lake Station has decreased, as well as larger individuals of both sexes. A hypothesis for this is that females and larger individuals are more vulnerable to predation by introduced mammals.

Introduction

New Zealand has one of the most diverse reptile assemblages of any temperate archipelago (Daugherty et al., 1990), but since the arrival of humans it has lost two species of lizards and many of the extant species have drastically reduced populations (Daugherty et al., 1994; Hitchmough et al., 2010). Predation by introduced mammals, especially kiore, *Rattus exulans* (Worthy and Holdaway, 2002), and habitat destruction (Towns and Daugherty, 1994) are thought to be the main reasons for the declines. Prior to human arrival New Zealand had no mammalian predators (Anderson, 1996; Holdaway, 1996; Worthy and Holdaway, 2002; Worthy et al., 2006). Now New Zealand has 11 species of introduced mammalian predators, of which all are known to eat lizards (Bettesworth, 1972; Bettesworth and Anderson, 1972; Cuthbert et al., 2000; Daugherty and Towns, 1991; Jones et al., 2005; King, 2005; Newman, 1994; Newman and

McFadden, 1990; Norbury, 2001; Worthy and Holdaway, 2002). Due to a mammalian predator-free evolutionary history (Anderson, 1996; Holdaway, 1996; Worthy and Holdaway, 2002; Worthy et al., 2006) New Zealand lizards evolved highly K-selected life history strategies (Bauer and Russell, 1986; Cree, 1994; Robb, 1986; Wilson, 2004). Most significantly all but one species of lizard in New Zealand is viviparous (Cree, 1994; Robb, 1986). This is extremely rare elsewhere in the world (Cree, 1994; Dunham et al., 1988). Due to being viviparous and the cool temperate climate, no species of lizard in New Zealand have multiple broods per year, unlike most lizard species elsewhere (Cree, 1994; Dunham et al., 1988). This makes New Zealand lizards very susceptible to disturbance as they have lower reproductive outputs than other species (Cree, 1994; Cree and Guillette Jr, 1995; Robb, 1986). To create effective conservation programs for threatened species of reptiles it is vital to understand their ecology and life history traits. Unfortunately, many of the basic life history traits are not well known for the majority of New Zealand's indigenous lizards, creating obstacles to conservation initiatives.

Three species of skink are known from Nelson Lakes National Park: northern grass skink (*Oligosoma polychroma*), speckled skink (*O. infrapunctatum*) and spotted skink (*O. lineoocellatum*). All three species are diurnal, give birth to live young and are indigenous to New Zealand (Whitaker, 2000). The northern grass skink is the most widespread species in Nelson and Marlborough. It typically lives in densely-vegetated grasslands or shrublands from near sea level to the subalpine zone (Whitaker, 2000). The northern grass skink in the Nelson Lakes area are from clade 1b (Liggins et al., 2008). The speckled skink is found in the central North Island, Nelson and Westland (Whitaker, 2000). It is localised and rare within the Nelson/Marlborough Conservancy where it is found on Stephens Island, and at isolated sites at Golden Downs and in the upper Buller catchment (Whitaker, 2000). Speckled skinks typically inhabit densely vegetated grassland, shrubland or fernland below 900 m (Whitaker, 2000). The spotted skink is found from Hawkes Bay to south Canterbury (Whitaker, 2000). It is widespread in Nelson and Marlborough east of the Waimea basin (Whitaker, 2000). It inhabits dry scrubby and rocky areas and subalpine grassland to at least 1600 m (Whitaker, 2000). The spotted skink clade from Nelson Lakes area is 1b (Greaves et al., 2007). All three species are on New Zealand Threat Classification List and are considered conservation dependant (Hitchmough et al., 2013). The speckled skink is listed on the New Zealand Threat Classification List as at risk, due to having a sparse population in partial decline (Hitchmough et al., 2013), and it is also listed on the

IUCN Red List as near threatened (IUCN, 2015). Although its overall area of occupancy is more than 100,000 ha at present, it is predicted to decline 10-70% (Hitchmough et al., 2013). The spotted skink clade 1b is considered a relict population, with more than 20,000 mature individuals and is stable or increasing (Hitchmough et al., 2013). However, these populations are sparse and some are in decline (Hitchmough et al., 2013)

While there has been research on the range and habitat preferences of these skink species, there has been limited research on basic life history traits, especially for speckled skinks (Table 2.1). Thus the objective of this study is to provide more information on the life history traits of northern grass, speckled, and spotted skinks in the St. Arnaud area of the Nelson Lake National Park.

Methods

Study area

I studied all three species of skink that are known to occur in the Rotoiti Nature Recovery Area (RNRP) and the surrounding area of the South Island, New Zealand. This area is dominated geologically by the Southern Alps and wide river valleys. Prior to human settlement the area was covered in beech forest (*Fuscosporia solondri, F. fusca* and *Lophozonia menziesii*) except for the alpine, river beds and wetlands. Natural forest cover still occurs within Nelson Lakes National Park, but presently much of the area outside the park is sheep and beef farmland. Live-capture pit-fall traps were set within the RNRP and at Lake Station (Figure 2.1). The RNRP is an 840 ha area adjacent to St. Arnaud within Nelson Lakes National Park in which, beginning in 2002, there has been ongoing control of introduced mammalian predators. Lake Station is a farm 12 km from St. Arnaud township that has been used since the 1970's for skink research (Spencer et al., 1998). Thus this study builds on the previous work done at the site.

Life history traits

During a live-trapping programme (see next section) I collected information on a variety of life history traits. First, I estimated the sex ratio in each species. All three species are readily sexed by visual inspection of genitalia. Females were checked for pregnancy by gently palpating between the thumb and fingers to feel for embryos (Hare et al., 2010). Deviations from unity are

common in the sex ratio of reptile populations, and may occur because of differences in the vulnerability of one sex to predation. Next, I took a series of morphological measurements to estimate the sizes of individuals in each population. I used snout to vent length (SVL) to estimate body size. The skink was then marked on its ventral side with a dot of a silver xylene-free permanent marker pen. A different location for the dot was chosen for each of the 10 days so that the day of capture could be determined on recapture. The dorsal and ventral side of each skink was photographed. It was then released at the point of capture. The above process took around three minutes. For northern grass skinks individuals < 42 mm were considered juvenile (Barwick, 1959; Spencer et al., 1998), while for spotted skinks individuals < 62 mm were considered juvenile (Spencer et al., 1998). To investigate the effects of weather on trapping success I used the weather data from the national weather database 'CliFlo' (NIWA, 2014).

I conducted a vegetation survey to investigate the effects of habitat type on speckled skink abundance. At each pit-fall trap location I took four 25 cm x 25cm square quadrat surveys. I divided the area around each trap into four equal areas and took a random quadrat sample from each of these four sections. To select sites I first generated two random numbers from 0 – 200; the first number was used as the x co-ordinate and the second as the y co-ordinate, giving the position of the corner of the quadrat closest to the trap in centimetres from the trap. I recorded the plant species present in the quadrat as well as the presence of bare ground and rocks. To analyse the data I grouped the data as: bare ground, grass, moss or lichen, rock, low shrub and shrub. Each trap was given a number of 1 (1-25% cover), 2 (26-50% cover), 3 (51-75% cover) or 4 (76-100% cover) as to the relative amount of each type of habitat present around the trap.

Trapping methods

Thirty eight pit-fall traps (Whitaker, 1967) were set in the RNRP in November 2002, coinciding with the onset of mammalian predator-trapping in that area (Figure 2.1). They were divided into two sites, RNRP1 and RNRN2, with 19 pit-fall traps in each (Figure 2.1). The traps were placed along roads and walking tracks.The exact location of each pit-fall trap was chosen based on areas that appeared to be favourable to skinks, thus they were placed in sunny, dry microhabitats. The traps were monitored each summer (November – March) from 2002 to 2012, except for the summer of 2009/2010. For the summers from 2002 to 2009 the traps were monitored over two to five trapping episodes of four days duration. For 2010-2012 monitoring sessions were

lengthened to 10 days and were conducted monthly. I collected the data from 2002 – 2007 and 2010-2012, while other FOR volunteers collected the data from 2007 – 2009. When possible trapping was conducted in good weather to maximise catch rates.

I expanded the project in 2010 to investigate populations outside of the RNRP were there is no predator control. I set 50 pit-fall traps at Lake Station in November 2010. The traps were divided evenly into two sites, LSA and LSB, with 25 in each site (Figure 2.1). These traps were spaced evenly within a 20 m^2 grid, with each trap five meters apart. These traps were checked during the same monitoring sessions as the traps within the RNRP. I chose Lake Station because it has been used historically for skink research (Spencer et al., 1998) and thus I could compare my results to past research.

The traps set in 2002 were constructed from 3 L canned fruit tins (24 cm x 16 cm). Square tin lids with folded down corners were placed over the top opening. This allowed skinks to crawl in, but kept the rain and sun out. A rock was placed on top to keep the lid on. The pit-falls traps set in 2010 at Lake Station were green 4 L plastic pails. To allow skinks to enter, a gap was created by laying sticks between the pail and the lid. The lid was held in place by a rock. Holes were drilled in the bottom of all pit-falls for water drainage. Each pit-fall trap was placed in the ground such that the top was flush with the soil. The bottom was covered with a thin layer of soil. Traps were then baited with a thumb-nail sized piece of canned pear. To maintain moisture a 7 cm x 5 cm x 0.5 cm kitchen sponge was moistened and placed in the trap. The sponges were washed prior to being used to remove any factory chemicals. On each day of monitoring the old bait was replaced by fresh bait and the sponge moistened. In traps where the sponge dried out within 24 hrs another sponge was added. On the last day of monitoring the traps were closed by filling them with sticks such that if a skink or other animal fell in it could climb out.

Statistical analyses

Data were analysed using the program R (R Core Team, 2013). The packages ‘gdata’ (Warnes et al., 2013), ‘lme4’ (Bates et al., 2013), 'AICcmodavg' (Mazerolle, 2013), ‘AER’ (Kleiber and Zeileis, 2015) and ‘nnet’(Ripley and Venables, 2015) were used. To explore the influence of vegetation and month on speckled skink catch rate, sex ratios and length (SVL) I compared ecologically relevant generalised linear mixed-effects models (glmer) using Akaike’s Information Criterion for small sample sizes (AICc Burnham and Anderson, 2002). Data from

RNRP2 was used as this was the site at which speckled skinks were most common. The random factors in all models were year and trap number.

To investigate whether differences in the catch rate of speckled skinks were correlated with vegetation type or month I compared models with binomial distributions. Catch or no catch was the dependant variable. The fixed factors were: month, and amount of bare ground, grass, shrub, low shrub, moss and lichen or rock within a two metre radius of the trap. The null model, all single factor, additive two factor and interactive two factor models were compared. Three way models were not compared as they were too complicated for the data and did not converge.

To test whether skink length is correlated with vegetation type or month I compared models with Gaussian distributions. SVL was the dependant variable. The fixed factors and models compared were the same as those used to investigate catch rates (above). To analyse whether the probability of catching a female or male skink is correlated with vegetation type I compared models with binomial distributions. Sex (female or male) was the dependant variable. The fixed factors were the same as for testing effects on SVL and catch rate except without month or grass. Month could not be added into the model comparisons because in December, February and March only female skinks were caught. Grass could not be compared as all models failed to converge. This was due to small sample sizes and only female skinks being caught in sites with 0% grass and only male skinks being caught in sites with 51-75% grass. In addition there were no sites with 26-50% grass or 76-100% grass. The null model, all single factor, additive two factor and interactive two factor models were compared.

Results

Northern grass skinks

In total, 767 northern grass skinks were caught over the 10 years of study, making them the most abundant lizard species in the area. The recapture rate was 1.7%. The sex ratio in northern grass skinks was not sex biased: with 1.0 female: 1.1 male: 0.8 juvenile. Juvenile was defined as < 42 mm (Barwick, 1959; Freeman, 1997). Analyses of individuals caught in my study from the Lake Station site also showed a fairly even sex ratio, slightly in favour of females (1.0 female: 0.9 male: 0.8 juvenile).

In this study, northern grass skinks ranged in SVL from 22 mm – 76 mm, with a mean of 49.6 mm. Both sexes at maturity (> 42 mm) in my study had similar SVLs, with males being only slightly longer (females 53.9 mm, males 54.7 mm), although individuals at the Lake Station site were a bit larger (female 58.2 mm, male 59.8 mm). I caught the most newborn skinks (< 30 mm; Barwick, 1959) during January (22), and February (11); I also caught newborns in November (2), December (6) and March (3). In addition I caught pregnant females in November (2), December (7), January (12), and February (3). The most northern grass skinks were caught in January, followed by November, December, February and March (Table 2.2).

Speckled skinks

Seventy six speckled skinks were caught, almost exclusively from RNRP2 (71 RNRP2, 5 Lake Station, 1 RNRP1). The recapture rate was 9.2%. The skinks ranged in SVL from 35 mm – 98 mm with a mean of 72.3 mm. Females were slightly smaller than males, with a SVL of 73.4 mm compared to 76.3 mm. The size of the smallest skink I captured was 35 mm (November 2007), with all others over 49 mm. Thirteen pregnant speckled skinks were caught, nine in November, two in December and two in January. The smallest pregnant female was 56 mm. The size at sexual maturity has not been previously defined for speckled skinks. These data suggests that the size at sexual maturity is > 55 mm and I classified individuals smaller than this as juveniles. Given these parameters the sex ratio is 1.0 female: 0.3 male: 0.1 juvenile.

The most common vegetation type within a 2 m radius of traps at site RNRP2 was moss and lichen which represented around 21% of the ground cover, followed by rock (20% of the ground cover), shrub (20% of the ground cover), bare ground (18% of the ground cover), large shrub (16% of the ground cover) and grass (6% of the ground cover). An AICc model comparison showed that the combination of the amount of shrub around a trap and the month had the greatest effect on the skink catch rate (AICc weight = 0.23; Table 2.3), followed by a model containing the amount of rock and month (AICc weight = 0.15; Table 2.3) and a model containing only month (AICc weight = 0.14; Table 2.3). The highest catch rate was in January, with a catch rate almost twice as high as the second highest catch rate—November (Table 2.2 & Figure 2.2). February had the lowest catch rate (Table 2.2 & Figure 2.2). For shrub habitats, no skinks were caught in traps with 0% or 1-25% shrub present (Figure 2.3). The catch rate was similar in traps with 26-50% and 51-75% shrub present, while the highest catch rate was in traps with 76-100%

shrub present (Figure 2.3). In regards to the amount of rock present around traps, the highest skink catch rate was in areas with 76- 100% rock present, followed by 1-25% rock, 51-75% rock and 26-50% rock (Figure 2.4). No skinks were caught in traps with no rock present within 2 m (Figure 2.4).

None of the factors investigated had a significant effect on the SVL (null model AICc weight = 0.20; Table 2.4) or the sex (null model AICc weight = 0.08; Δ AIC = 0.69; Table 2.5) of speckled skinks caught. Only female skinks were caught in December and March, but this is not unexpected due to the high proportion of females in the population and the low sample size. Likewise, traps with no grass within a 2 m radius only caught female skinks while traps with 51-75 % grass around them only caught male skinks. As only 3 skinks and 1 skink were caught in these two categories respectively, this is probably due to sample size and a female population bias, as compared to any differences in habitat preferences between sexes.

Spotted skinks

Few spotted skinks were caught (16 total, 5 from RNRP2; all prior to 2008 and 11 from Lake Station). There were no recaptures. The sex ratio for spotted skinks was highly skewed towards females, with half of the population being juveniles (1.0 female: 0.2 male: 1.5 juvenile). Spotted skinks in this study ranged in SVL from 35 mm – 87 mm, with a mean of 60.3 mm. Spotted skinks were most often caught in November and March, followed by February, December and January (Table 2.2). The smallest I caught was 35 mm. The three skinks under 40 mm were caught in March. I did not catch any pregnant females.

Discussion

Northern grass skinks

The demographics of the northern grass skink population in the Nelson Lakes area appear to have changed significantly over the past 30 years. The sex ratio in this study at Lake Station (1.0 female: 0.9 male : 0.8 juvenile) is very different to the strongly female skewed ratio (3 female: 1 male: 1 juvenile) found in a previous study using collected specimens from 1970 at Lake Station (Spencer et al., 1998), a study in Canterbury (2.3 female: 1 male; Freeman, 1997) and coastal Canterbury (3 female: 1 male; Lettink and Seddon, 2007). All of these studies also used pit-fall trapping. A hypothesis for the changes seen in female to male sex ratios is that females are more

vulnerable to predation. When pregnant, females may be more susceptible to predation as they are heavier and less agile and may require more time foraging and/or basking (Bauwens and Thoen, 1981; Shine, 1980; Sinervo et al., 1991). Thus, over time fewer females will be seen in the population.

The SVL of skinks in this study is similar to that found in Canterbury (31 mm – 66 mm, Freeman, 1997; 25 mm – 65 mm, Lettink and Seddon, 2007). The smaller percentage of larger skinks caught in my study compared to 1970 (Figure 2.5; Spencer et al., 1998) is potentially due to predation as larger individuals may be more susceptible to predation (Whitaker, 1978) or simply the skinks are not living as long. The exact method of capture in 1970 is unknown (Spencer et al., 1998), thus the lack of small (< 30 mm; Figure 2.5) individuals may be due to them not being captured. For example, the drain holes in the bottom of the pit-fall traps may have been large enough for small skinks to escape through. It is unlikely that small individuals were absent in 1970 because other than the lack of small skinks, the population seemed well distributed (Figure 2.5; Spencer et al., 1998). The reason for the increase in male northern grass skink SVL is unknown, but may be due male skinks living longer than they used to, or smaller adult male skinks being more vulnerable to predation than larger male skinks; additionally, it could be an artefact of sample size (19 males 2010-2012, 32 males 1970; Spencer et al., 1998).

Northern grass skinks are thought to be born in January and February (Barwick, 1959; Freeman, 1997; Gill, 1976; Patterson and Daugherty, 1990). While I caught the most newborn skinks (< 30 mm; Barwick, 1959a) during January and February, I also caught newborns in November, December and March. In addition I caught pregnant females in November though until February. This suggests that they have a breeding period of November to March in the Nelson Lakes area, which is longer than elsewhere. There was very little difference between the percentage of juveniles caught in this study (29%) and 1970 (24%; Spencer et al., 1998). Of interest, the smallest pregnant female was 55 mm, significantly larger than the cut off of 42 mm for juvenile size (Barwick, 1959; Spencer et al., 1998). Thus either females have started breeding later in this area, or I simply did not catch any young pregnant skinks, or if I did, I was unable to identify that they were pregnant.

Speckled skinks

Little previous research has been done on the life history traits of speckled skinks. Little research exists on the size of speckled skinks. This study found them to range from 35 – 98 mm SVL, with the mean female SVL 73.4 mm and the mean male SVL 76.3 mm (with adult defined as > 55 mm). The size at birth of speckled skinks does not appear recorded in the literature. The size of the smallest I captured was 35 mm. Thirteen pregnant speckled skinks were caught, nine in November, two in December and two in January, suggesting a breeding season of November to January. The size at sexual maturity has not been previously defined for speckled skinks. This data suggests that the size at sexual maturity is > 55 mm and I classified individuals smaller than this as juveniles. Given these parameters the sex ratio is 1.0 female: 0.3 male: 0.1 juvenile. Similarly, Lettink and Seddon (2007) also found a highly female biased sex ratio (7 female: 1 male). Size at sexual maturity may actually be significantly smaller than 55 mm for this species, and more research needs to be done to accurately define size at sexual maturity. Given that for both speckled and spotted skinks large/older individuals are more trappable than juveniles (Efford *et al*., unpubl. data), the proportion of juveniles in the population may be higher than the data shows.

The catch rate for speckled skinks was the highest in January, followed by November. This is probably due to these months being the hottest and driest in Nelson Lakes National Park (NIWA, 2014) which are weather conditions found to be favourable to skinks (Hoare et al., 2009). Other research has also shown speckled skinks to prefer areas with lots of shrub present (East et al., 1995). This may be due to shrubs providing a food source and/or refugia from predators. Fruits and flowers make up a substantial part of the diet of most skinks species in New Zealand (Freeman, 1997; Olesen and Valido, 2003; Patterson, 1992; Spencer et al., 1998). Although the diet of speckled skinks is unknown, it is likely to be very similar to other *Oligosoma* species. Shrubs provide protection from avian predators, and potentially tuatara as well, which would have been a natural predator before they became extinct from the mainland (East et al., 1995; Towns and Daugherty, 1994). Shrubbery probably provides little protection from mammalian predators, which are present in this habitat (King, 2005).

Like shrub habitats, catch rate varied significantly in regards to percentage of rock present within a 2 m radius of the trap and the month. The general preference for large amounts of rock present,

and no skinks caught at traps without any rock in a 2 m radius, is expected as rock provides basking and hiding locations. The reason for the preference of sites with 1-25% rock over areas with higher rock coverage is not known. It may be due to those areas having a greater coverage of another preferred vegetation type, such as shrubbery. More research is needed to investigate this.

Spotted skinks

The life history traits of the spotted skink population in the Nelson Lakes area appear to have stayed fairly constant over the past 30 years. The sex and age ratio of spotted skinks in 1970 was also female dominated with about 1/3 juveniles (1.0 female: 0.7 male: 0.8 juvenile; Spencer et al., 1998). This differs from 1995 when it was 7 adults: 1 juvenile (Efford et al., unpubl. data). Given larger/older individuals are more trappable than juveniles (Efford *et al*., unpubl. data), the proportion of juveniles in the population may be higher than the data shows. Spotted skinks in this study ranged in SVL from 35 mm – 87 mm, with a mean of 60.3 mm. Little previous research exists on the size of this species, but SVL has previously been broadly described as between 80 – 90 mm (Jewell, 2011). In both this study and that by Efford et al. (unpubl. data), spotted skinks were the most trappable in spring and autumn, with the fewest caught in December and January. The size at birth for spotted skinks has not been well defined. Robb (1986) found newborns to be about half adult size. Combining this with juveniles being defined as < 62 mm (Spencer et al., 1998), newborns should be around 30 mm. The smallest I caught was 35 mm. Spotted skinks are known to give birth between February and March (Robb, 1986), which my data supported as the three skinks under 40 mm were caught in March.

Recapture rates

There were few recaptures within the 5-10 day monitoring intervals (1.7% for northern grass skinks, 9.2% for speckled skinks and 0% for spotted skinks). Similarly, Freeman (1997) found a 4% recapture rate for northern grass skinks, while at Pukerua Bay it was found to range from 11% - 44% depending on the year (Towns and Elliott, 1996). The years with the lowest recaptures corresponded to years with increased predation (Towns and Elliott, 1996). Similarly, Lettink et al. (2011) had a 33% recapture rate in the first year of the study, which decreased to 5% in the second year, for unknown reasons. The recapture rate for speckled skinks at Lake Station in 1995 was 50.4% (Efford *et al*., unpubl. data). For spotted skinks the recapture rate was

37% in 1995 (Efford *et al*., unpubl. data), and similarly on Stephens Island, it was 48% (Stephens, 2004). My low catch of speckled and spotted skinks probably explains my low recapture rates.

Conclusion

Life history information is vital in creating well-designed conservation initiatives as it allows species managers to tailor efforts in accordance with species-specific ecological factors, such as breeding seasons and behavioural differences between species. This study has added to the existing knowledge of the life history traits of speckled, northern grass and spotted skinks. I estimated the size at sexual maturity and birthing season for speckled skinks (Table 2.6). Though values defined are estimates and may be specific to the St. Arnaud area, future research from other locations can build on these values, painting a more complete picture of the ecology of these species. In addition, this work adds to the understanding of speckled skink habitat preferences. It supports the findings of other work that also showed shrubbery to be an important habitat and added the information that the presence of rock may also be important. My findings that the months with the highest catch rate varied by species, as has also been found in previous work, highlights the challenges of using catch rates to understand population demographics and compare populations.

Since the 1970's the proportion of female northern grass skinks caught at Lake Station has decreased, as well as the numbers of large individuals of both sexes. A hypothesis for these changes is that females and larger individuals are more vulnerable to predation. This illustrates how life history information can allow managers to identify demographic changes over time and between areas, which may indicate problems within the population, or show the success of the conservation efforts.

Figures and Tables

Table 2.1: Summary of known demographics for each species; [1]Barwick (1959), [2]Freeman (1997), [3]Grill (1976), [4]Jewel & Morris (2011), [5]Patterson and Daugherty (1990), [6]Robb (1986) and [7]Spencer et al. (1998).

Species	Sex ratio female:male	SVL range (mm)	♀ μ SVL (mm)	♂ μSVL (mm)	Newborn size (mm)	Juvenile size (mm)	Birthing season
Northern grass	3:1[7], 2.3:1[2]	31-66[2]	56.74[7]	51.72[7]	< 30[1]	< 42[1,2]	Nov–Feb[1,2,3,5]
Speckled	?	adult μ 80-106[4]	?	?	?	?	?
Spotted	1.6:1[7]	adult μ 80-90[4]	70.1[7]	76.3[7]	?	< 62 [2,7]	March[6]

Table 2.2: The number of northern grass, speckled and spotted skinks caught per trap day by month. The highest catch rate for each species is in bold font.

Month	Northern grass	Speckled	Spotted
November	0.0369	0.0051	**0.0012**
December	0.0336	0.0022	0.0005
January	**0.0568**	**0.0080**	0.0002
February	0.0251	0.0011	0.0007
March	0.0167	0.0018	**0.0012**

Table 2.3: AICc comparison of models used to evaluate variables as predictors of the catch rate of speckled skinks. Each vegetation type (Bare Ground, Grass, Moss & Lichen, Rock, Shrub and Low Shrub) refers to the amount of that vegetation type within a 2 m radius of the trap.

Model	K	AICc	ΔAICc	AICc Weight	Cumulative Weight	Log Likelihood
Shrub + Month	8	451.75	0	0.23	0.23	-217.85
Rock + Month	8	452.63	0.88	0.15	0.38	-218.29
Month	7	452.77	1.02	0.14	0.52	-219.37
Moss & Lichen + Month	8	453.96	2.21	0.08	0.59	-218.95
Grass + Month	8	454.11	2.35	0.07	0.66	-219.03
Bare Ground + Month	8	454.4	2.65	0.06	0.72	-219.17
Low Shrub + Month	8	454.77	3.02	0.05	0.78	-219.36
Bare Ground * Rock	6	456.27	4.52	0.02	0.8	-222.12
Shrub + Rock	5	456.29	4.54	0.02	0.82	-223.13
Shrub * Rock	6	456.56	4.8	0.02	0.84	-222.26
Bare Ground * Shrub	6	456.79	5.04	0.02	0.86	-222.38
Shrub	4	457.29	5.54	0.01	0.88	-224.64
Rock	4	458.18	6.43	0.01	0.89	-225.08
Bare Ground + Shrub	5	458.24	6.48	0.01	0.9	-224.11
Null	3	458.31	6.56	0.01	0.9	-226.15
Shrub * Low Shrub	6	458.45	6.7	0.01	0.91	-223.21
Grass + Shrub	5	458.76	7	0.01	0.92	-224.37
Shrub + Moss & Lichen	5	458.97	7.22	0.01	0.93	-224.48
Shrub + Low Shrub	5	459.23	7.48	0.01	0.93	-224.6
Bare Ground + Rock	5	459.29	7.54	0.01	0.94	-224.64
Moss & Lichen + Rock	5	459.3	7.55	0.01	0.94	-224.64
Moss & Lichen	4	459.5	7.74	0	0.95	-225.74
Bare Ground * Moss & Lichen	6	459.52	7.77	0	0.95	-223.74
Grass	4	459.65	7.89	0	0.96	-225.82
Shrub * Moss & Lichen	6	459.72	7.97	0	0.96	-223.85
Grass + Rock	5	459.81	8.06	0	0.96	-224.89
Low Shrub + Rock	5	459.85	8.1	0	0.97	-224.92
Bare Ground	4	459.94	8.18	0	0.97	-225.96
Low Shrub	4	460.31	8.55	0	0.97	-226.15
Moss & Lichen * Rock	6	460.51	8.76	0	0.98	-224.24
Bare Ground + Moss & Lichen	5	460.62	8.86	0	0.98	-225.3
Grass * Shrub	6	460.63	8.87	0	0.98	-224.3
Grass + Moss & Lichen	5	460.89	9.14	0	0.99	-225.44
Bare Ground + Grass	5	461.43	9.68	0	0.99	-225.7
Low Shrub + Moss & Lichen	5	461.49	9.74	0	0.99	-225.74
Grass * Rock	6	461.51	9.75	0	0.99	-224.74
Grass + Low Shrub	5	461.61	9.85	0	0.99	-225.79
Low Shrub * Rock	6	461.71	9.96	0	0.99	-224.84
Grass * Moss & Lichen	6	461.91	10.15	0	1	-224.94
Bare Ground + Low Shrub	5	461.93	10.18	0	1	-225.96
Grass * Low Shrub	6	462.87	11.11	0	1	-225.42
Bare Ground * Grass	6	463.16	11.41	0	1	-225.57
Low Shrub * Moss & Lichen	6	463.36	11.6	0	1	-225.66
Bare Ground * Low Shrub	6	463.92	12.17	0	1	-225.95

Table 2.4: AICc comparison of models used to evaluate variables as predictors of the SVL of speckled skinks. Each vegetation type (Bare Ground, Grass, Moss & Lichen, Rock, Shrub and Low Shrub) refers to the amount of that vegetation type within a 2 m radius of the trap.

Model	K	AICc	ΔAICc	AICc Weight	Cumulative Weight	Log Likelihood
Null	4	-65.23	0	0.2	0.2	36.9
Shrub	5	-65.08	0.15	0.18	0.38	37.97
Bare Ground * Shrub	7	-64.32	0.91	0.12	0.5	39.98
Shrub + Low Shrub	6	-62.94	2.29	0.06	0.56	38.08
Grass * Shrub	7	-62.65	2.58	0.05	0.62	39.15
Shrub * Low Shrub	7	-62.37	2.86	0.05	0.67	39.01
Shrub * Moss & Lichen	7	-61.92	3.31	0.04	0.7	38.78
Grass	5	-61.82	3.41	0.04	0.74	36.34
Grass + Shrub	6	-61.64	3.59	0.03	0.77	37.43
Shrub * Rock	7	-61.24	3.99	0.03	0.8	38.44
Bare Ground	5	-61.13	4.1	0.03	0.82	35.99
Grass * Rock	7	-61.02	4.21	0.02	0.85	38.33
Rock	5	-60.66	4.57	0.02	0.87	35.76
Shrub + Rock	6	-60.56	4.67	0.02	0.89	36.89
Low Shrub	5	-60.53	4.7	0.02	0.9	35.69
Bare Ground + Shrub	6	-60.32	4.91	0.02	0.92	36.77
Moss & Lichen	5	-60.2	5.03	0.02	0.94	35.53
Shrub + Moss & Lichen	6	-59.93	5.3	0.01	0.95	36.57
Grass * Low Shrub	7	-59.23	6	0.01	0.96	37.44
Bare Ground + Grass	6	-57.66	7.57	0	0.97	35.44
Grass + Low Shrub	6	-57.38	7.85	0	0.97	35.3
Grass + Rock	6	-57.24	7.99	0	0.97	35.23
Grass + Moss & Lichen	6	-56.82	8.41	0	0.98	35.02
Grass * Moss & Lichen	7	-56.74	8.49	0	0.98	36.2
Bare Ground * Grass	7	-56.65	8.58	0	0.98	36.15
Bare Ground + Rock	6	-56.48	8.75	0	0.98	34.85
Low Shrub + Rock	6	-56.38	8.85	0	0.99	34.8
Bare Ground + Low Shrub	6	-56.19	9.04	0	0.99	34.7
Bare Ground + Moss & Lichen	6	-56.07	9.16	0	0.99	34.64
Low Shrub * Rock	7	-55.65	9.58	0	0.99	35.65
Moss & Lichen + Rock	6	-55.64	9.59	0	0.99	34.43
Low Shrub + Moss & Lichen	6	-55.53	9.7	0	0.99	34.37
Bare Ground * Rock	7	-55.38	9.85	0	1	35.51
Bare Ground * Low Shrub	7	-55.32	9.91	0	1	35.48
Moss & Lichen * Rock	7	-54.46	10.77	0	1	35.05
Low Shrub * Moss & Lichen	7	-54.07	11.16	0	1	34.86
Bare Ground * Moss & Lichen	7	-53.57	11.66	0	1	34.61
Month	8	-45.68	19.55	0	1	31.91
Shrub + Month	9	-44.71	20.52	0	1	32.72
Grass + Month	9	-42	23.23	0	1	31.36
Bare Ground + Month	9	-41.88	23.35	0	1	31.3
Rock + Month	9	-41.19	24.04	0	1	30.96
Low Shrub + Month	9	-40.68	24.55	0	1	30.7
Moss & Lichen + Month	9	-40.6	24.63	0	1	30.66

Table 2.5: AICc comparison of models used to evaluate variables as predictors of the sex of a speckled skink that was captured. Each vegetation type (Bare Ground, Moss & Lichen, Rock, Shrub and Low Shrub) refers to the amount of that vegetation type within a 2 m radius of the trap.

Model	K	AICc	ΔAICc	AICc Weight	Cumulative Weight	Log Likelihood
Bare Ground + Moss & Lichen	5	70.19	0	0.12	0.12	-29.58
Low Shrub * Moss & Lichen	6	70.6	0.41	0.1	0.22	-28.56
Bare Ground * Moss & Lichen	6	70.72	0.53	0.09	0.31	-28.63
Shrub * Low Shrub	6	70.78	0.59	0.09	0.4	-28.66
Null	3	70.89	0.69	0.08	0.48	-32.24
Shrub + Low Shrub	5	71.15	0.96	0.07	0.55	-30.06
Shrub	4	71.77	1.57	0.05	0.61	-31.55
Moss & Lichen	4	71.96	1.76	0.05	0.66	-31.64
Shrub + Moss & Lichen	5	72.29	2.09	0.04	0.7	-30.63
Rock	4	72.33	2.13	0.04	0.74	-31.82
Moss & Lichen + Rock	5	72.77	2.58	0.03	0.77	-30.87
Bare Ground	4	72.98	2.78	0.03	0.8	-32.15
Low Shrub	4	73.14	2.94	0.03	0.83	-32.23
Shrub + Rock	5	73.28	3.09	0.03	0.86	-31.12
Bare Ground * Low Shrub	6	73.98	3.78	0.02	0.87	-30.25
Bare Ground + Shrub	5	74.1	3.9	0.02	0.89	-31.53
Shrub * Moss & Lichen	6	74.1	3.9	0.02	0.91	-30.31
Low Shrub + Moss & Lichen	5	74.32	4.12	0.02	0.92	-31.64
Low Shrub + Rock	5	74.61	4.41	0.01	0.94	-31.79
Bare Ground + Rock	5	74.67	4.47	0.01	0.95	-31.82
Moss & Lichen * Rock	6	74.78	4.58	0.01	0.96	-30.65
Shrub * Rock	6	75.01	4.81	0.01	0.97	-30.77
Low Shrub * Rock	6	75.11	4.92	0.01	0.98	-30.82
Bare Ground + Low Shrub	5	75.28	5.09	0.01	0.99	-32.12
Bare Ground * Shrub	6	76.16	5.97	0.01	1	-31.35
Bare Ground * Rock	6	77.02	6.82	0	1	-31.77

Table 2.6: Summary of demographics for each species caught in this study. All values defined in this paper unless indicated as from [1]Barwick (1959), [2]Freeman (1997), [3]Grill (1976), [4]Patterson and Daugherty (1990), [5]Robb (1986) or [6]Spencer et al. (1998), * indicates that the value is an estimate based on the data from this study and the true size may be smaller.

Species	Number caught	Sex ratio female:male:juvenile	SVL range (mm)	♀ μ SVL (mm)	♂ μ SVL (mm)	Newborn size (mm)	Juvenile size (mm)	Birthing season
Northern grass	767	144:156:109	22-69	53.9	54.7	< 30[1]	< 42[1,2]	Nov–Feb[1,2,3,4]
Speckled	76	48:13:3	35-98	73.4	76.3	< 35*	< 55*	Nov– Jan
Spotted	16	6:1:9	35-87	76	80	< 35*	< 62 [2]	March[5]

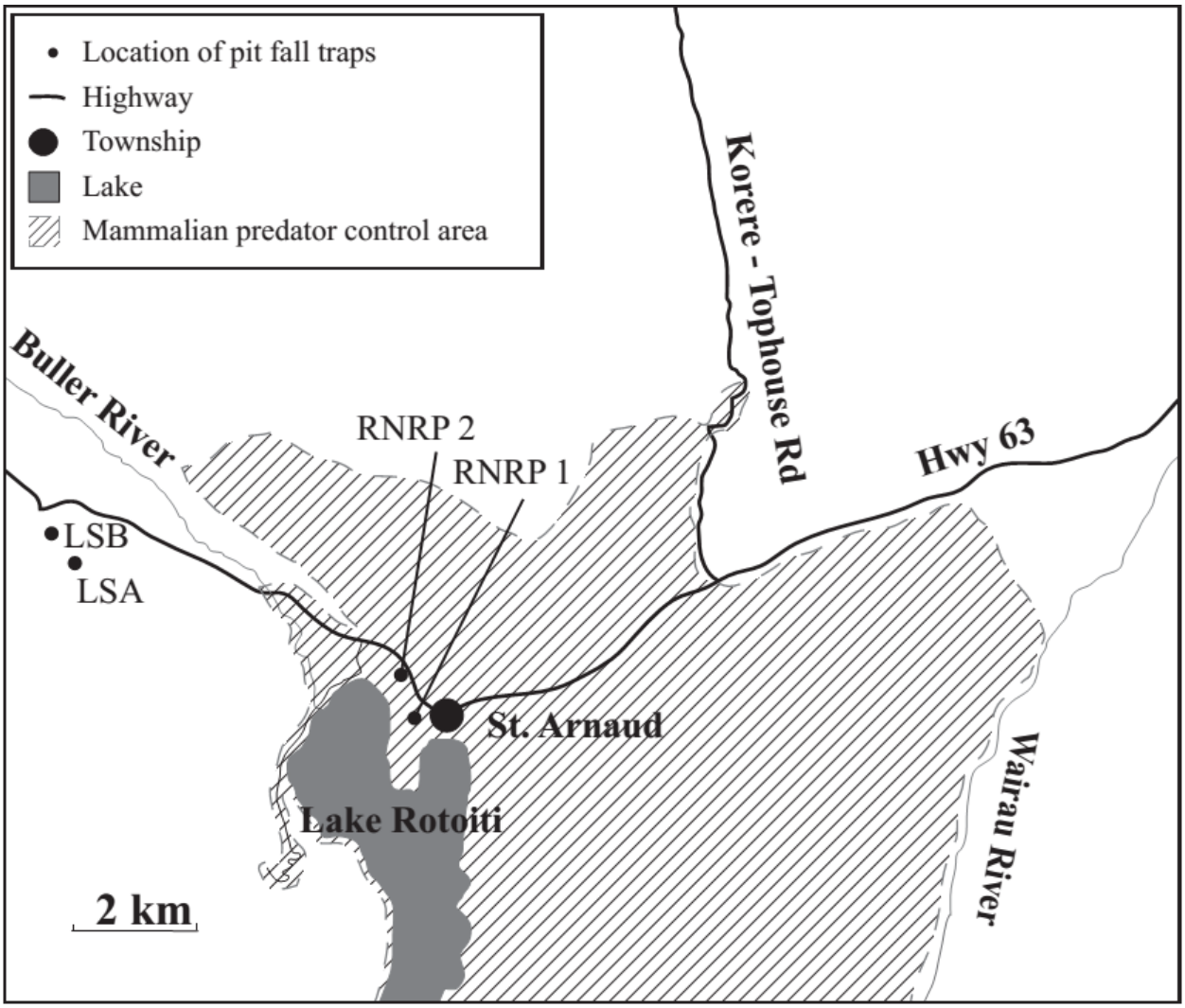

Figure 2.1: Map of the St. Arnaud area, showing the location of skink pit-fall traps and the mammalian predator control area.

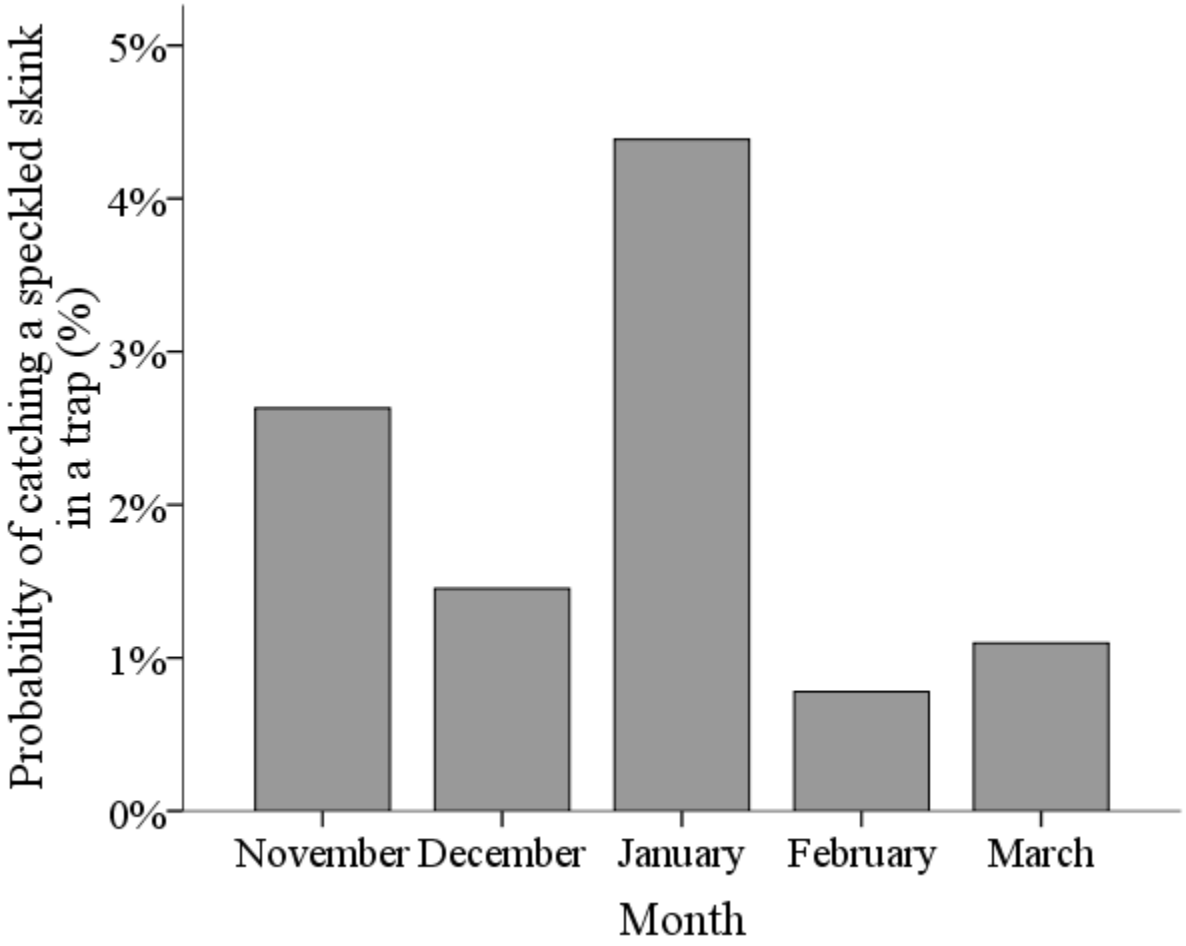

Figure 2.2: Relationship between the probability of catching a speckled skink in a trap and the month.

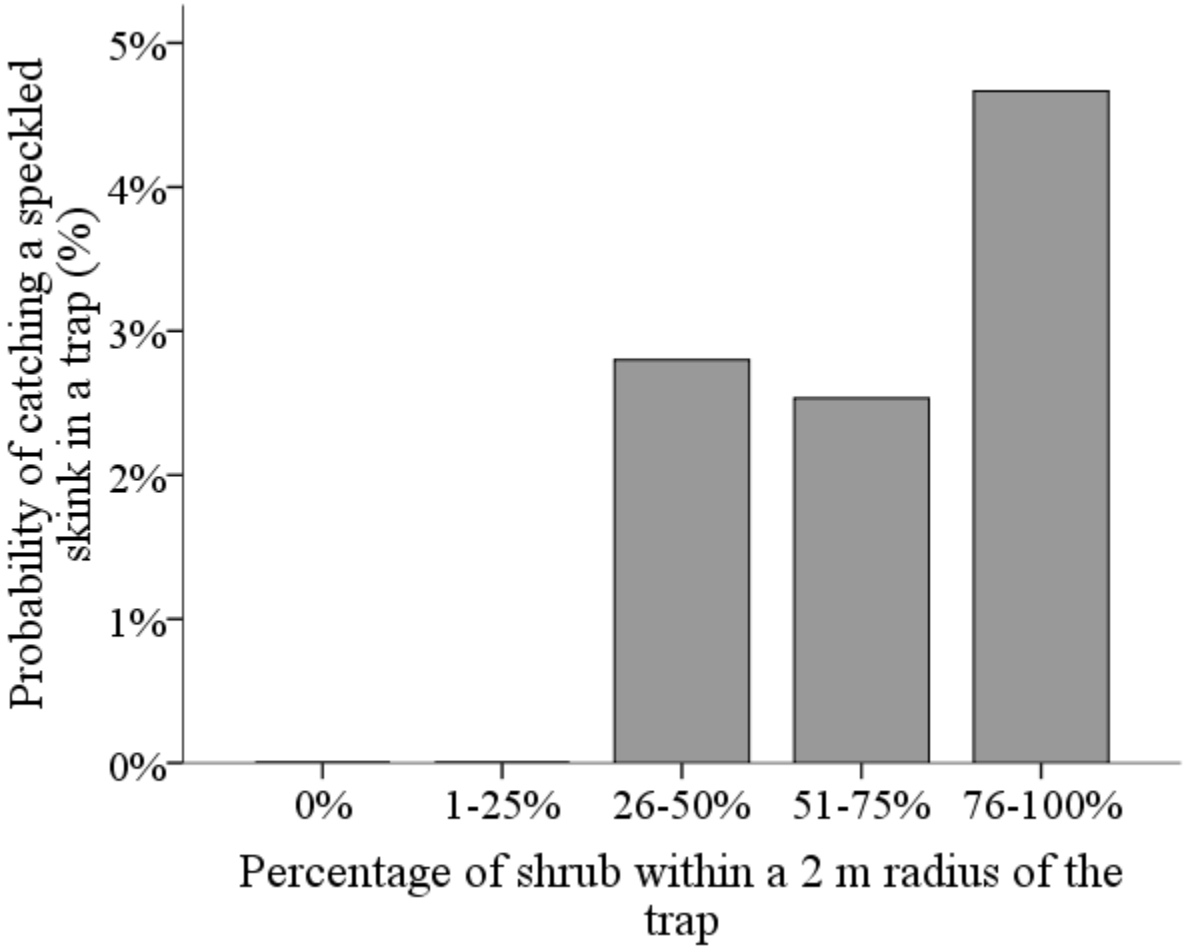

Figure 2.3: Relationship between the probability of catching a speckled skink in a trap and the amount of shrub within a 2 m radius of the trap.

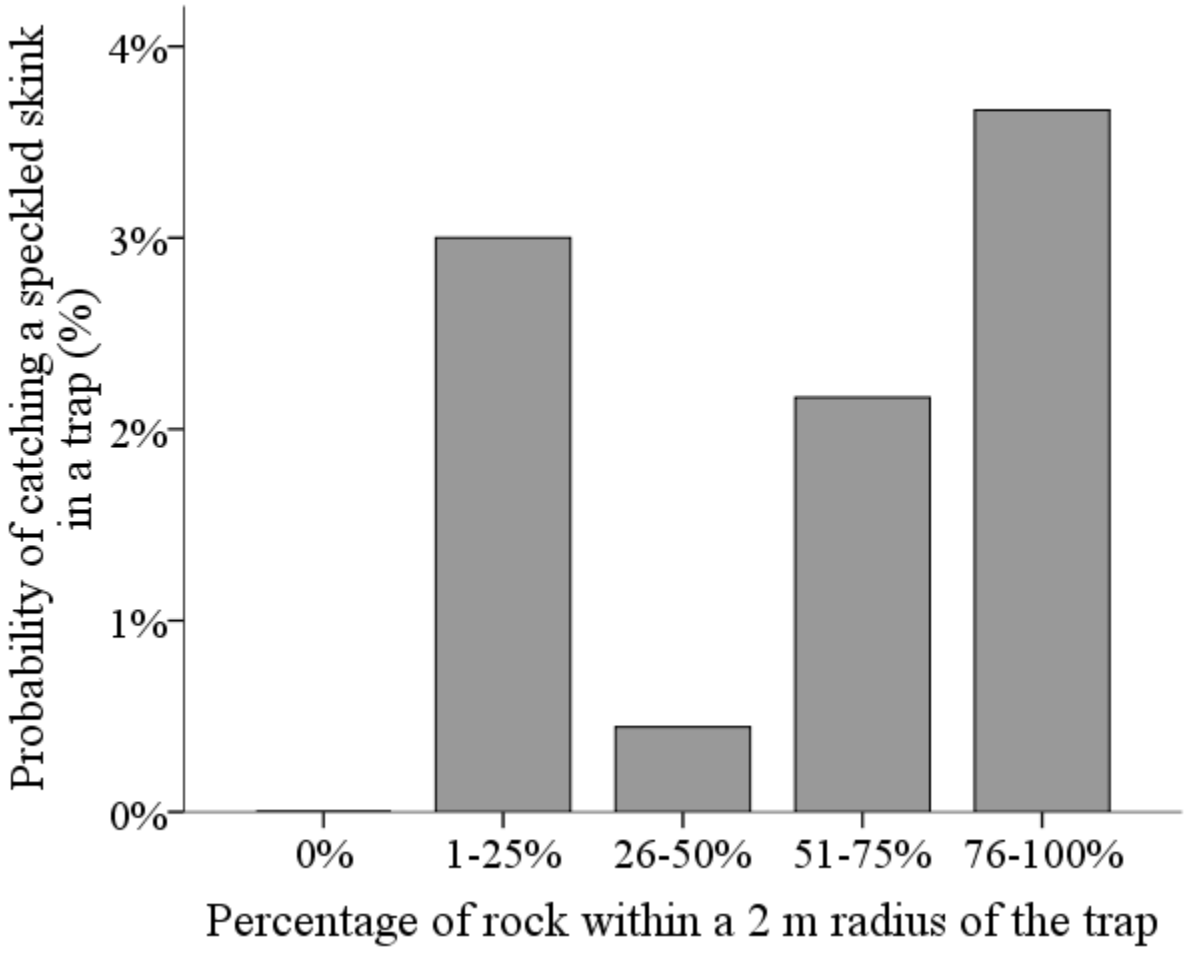

Figure 2.4: Relationship between the probability of catching a speckled skink in a trap and the amount of rock within a 2 m radius of the trap.

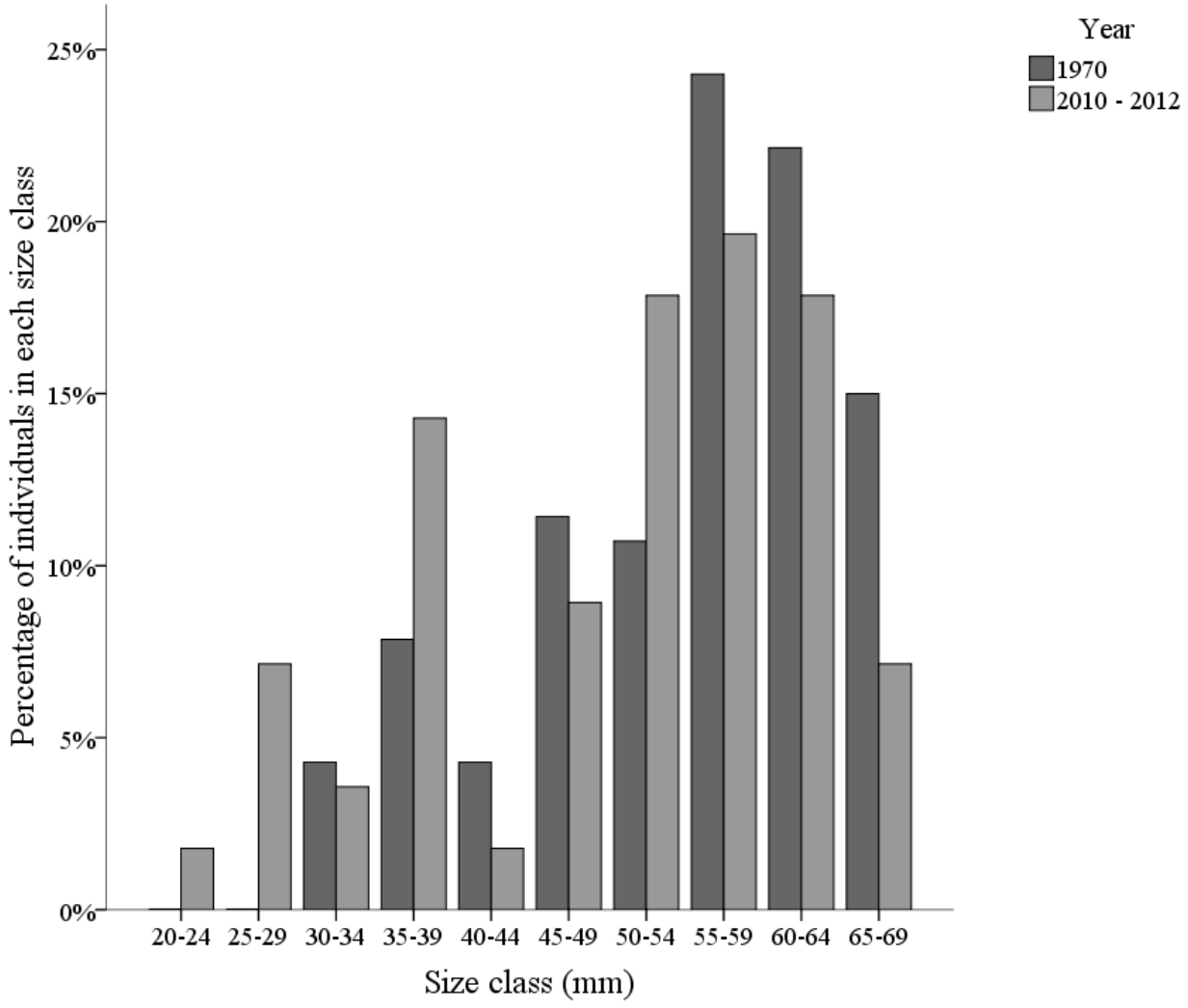

Figure 2.5: The percentage of northern grass skinks at Lake Station in each size class (mm) from 1970 (Spencer et al., 1998) and 2010-2012 (this study). Sample size: 1970 = 140 (Spencer et al., 1998), 2010-2012 = 56.

Chapter 3: Slithering away - a decade of mammalian predator trapping has not resulted in recovery of native skink populations

Abstract

Protection of indigenous lizard populations from introduced mammalian predators is a major conservation challenge in New Zealand. The Rotoiti Nature Recovery Project (RNRP) was established within the Nelson Lakes National Park in 1997 as a Department of Conservation 'mainland island'. In 2001 the control area was increased to include the habitat of the indigenous northern grass (*Oligosoma polychroma*), speckled (*O. infrapunctatum*) and spotted (*O. lineoocellatum*) skinks. I monitored these populations within the RNRP using live capture pit-fall traps during 2002 – 2012. Over the 10 years the northern grass and speckled skink populations have decreased significantly. Very few spotted skinks were found, though in the two sites that they were present they appeared to be in decline. In addition, the skink population on a farm outside of the RNRP has also shown substantial decline in all species since 1995. This study contributes to understanding of population trends of northern grass, speckled and spotted skinks and the intensity of mammal control required to protect these vulnerable lizard populations on the mainland.

Introduction

New Zealand has one of the most diverse endemic reptile assemblages of any temperate archipelago (Daugherty et al., 1990). It has around 109 species of lizard (Hitchmough et al., 2010) and the only species of tuatara (Jewell, 2011). Since the arrival of humans 1250-1300 years ago (Anderson, 1991; Wilmshurst and Higham, 2004), it has lost two species of lizards and many of the extant species have drastically reduced populations (Daugherty et al., 1994; Hitchmough et al., 2010). Under the New Zealand Threat Classification System List of endemic

species, 32 species of reptiles are listed as threatened and 50 species as at risk (Hitchmough et al., 2013). Many species are also listed as threatened globally (IUCN, 2015). In addition, many of New Zealand's reptile species have restricted present distributions (Bull and Whitaker, 1975; Towns and Daugherty, 1994; Worthy, 1987c), with 37% of New Zealand's lizard species (Towns et al., 2001) and tuatara (Bull and Whitaker, 1975) restricted to offshore islands. There is strong evidence that all but two lizard species (Grigg et al., 1985) once had much larger distributions (Bull and Whitaker, 1975; Cassels, 1984; Towns and Daugherty, 1994; Worthy, 1987c). No evidence of range reductions in reptiles prior the arrival of humans has been found (Towns and Daugherty, 1994).

The main hypothesis for the observed range contractions and extinctions are predation by introduced mammals, especially the kiore, *Rattus exulans* (Worthy and Holdaway, 2002), and habitat destruction (Towns and Daugherty, 1994). New Zealand has more species of introduced mammalian predators (11) than any other archipelago (Towns et al., 1997). The kiore and dog (*Canis familiaris*) were introduced by the Māori around 1000 years ago. Between 1790 and 1886 Europeans introduced: pigs (*Sus scrofa*), Norway rats (*R. norvegicus*), mice (*Mus musculus*), cats (*Felis catus*), ship rats (*R. Rattus*), possums (*Trichosurus vulpecula*), ferrets (*Mustela furo*), hedgehogs (*Erinaceus europaeus occidentalis*), weasels (*M. nivalis vulgaris*) and stoats (*M. erminea*) (Towns and Daugherty, 1994). All these species are known to eat lizards (Bettesworth, 1972; Bettesworth and Anderson, 1972; Cuthbert et al., 2000; Daugherty and Towns, 1991; Jones et al., 2005; King, 2005; Newman, 1994; Newman and McFadden, 1990; Norbury, 2001; Worthy and Holdaway, 2002).

The biological characteristics of many of New Zealand's indigenous herpetofauna species (such as their large size, low reproductive output, slow maturation and ground foraging behaviour) make them highly vulnerable to predation by introduced mammals. New Zealand skinks generally produce 1-5 offspring per female per year and all but one species is viviparous. The northern grass skink (*Oligosoma polychroma*) has an annual mean brood size of 3.8 to 5.13, depending on the region (Barwick, 1959; Patterson and Daugherty, 1990). Similarly, the speckled skink (*O. zelandicum*) has an annual brood size of 5.29 (Gill, 1976). These rates are relatively low compared to continental species and means that populations cannot cope with the high rates of predation caused by introduced predators (Cree, 1994; Cree and Guillette Jr, 1995;

Robb, 1986). Mammalian predators may also compete with reptiles for food (Tyrrell et al., 2000) as invertebrates and soft fruits are an important food source for both rodents (Best, 1969; Bettesworth, 1972; Daniel, 1973) and lizards (Whitaker, 1978).

The arrival of introduced mammalian predators has substantial effects on lizard populations in New Zealand. This has been especially well documented in rats which are probably one of the most serious of the introduced predators for lizards as they are widespread and at times abundant. The arrival of rats on islands is correlated with a rapid decline in the density and diversity of the lizard fauna (McCallum, 1986; Towns and Daugherty, 1994). Islands without rats can have up to 20 fold higher densities of lizards than islands with rats, as well as a higher diversity of species (Parrish and Pierce, 1993; Towns, 1991; Whitaker, 1973). The extermination of rats from islands typically results in increased lizard abundance and range (Towns, 1991, 1996, 2009). The species showing the most rapid response has been the shore skink (*O. smithi*), with a 3600% increase over 9 years (Towns, 1994, unpubl. data). Following the removal of rats, many lizard species presumed to have originally existed on the islands have been reintroduced, with excellent success. This shows their absence is due to predation not lack of suitable habitat (Hicks et al., 1975; Taylor and Thomas, 1993; Thomas and Whitaker, 1995; Towns, 1994; Towns and Ferreira, 2001). Overseas, the introduction of domestic cats (Gibbons and Watkins, 1982; Nogales et al., 2006; Vinson and Vinson, 1969) and dogs (Iverson, 1978) has been documented to cause the decline and extinction of reptiles from islands. Therefore, these species, as well as the other introduced mammalian predators in New Zealand, are likely to have caused similar detrimental effects on New Zealand lizard populations.

To increase biodiversity on the mainland, the Department of Conservation has initiated six ‘mainland islands’. These are areas in which introduced pest species, especially mammalian predators, are heavily controlled or totally removed. The objective of the mainland island project is to replicate the success of offshore islands in the recovery of endangered species, and although birds are the main target in most mainland island projects, it is thought that reptile populations would also benefit and recover. This study investigates the dynamics of three skink species inside the Rotoiti Nature Recovery Project (RNRP), a mainland island, for a decade after its commencement. In addition, I conducted a two year survey of the skink populations at Lake Station, a site that has been used historically for skink research (Efford, 2014a; Spencer et al.,

1998). Thus I was able to compare my results to those from 1995 (Efford et. al. unpubl. data) to investigate long term trends both inside and outside of the RNRP. My aim was to determine whether the control of introduced mammalian predators in the RNRP has led to a recovery of skink populations, and compare this to populations outside of the RNRP.

Methods

Three species of skink are known to from Nelson Lakes National Park: northern grass skink (*Oligosoma polychroma*), speckled skink (*O. infrapunctatum*) and spotted skink (*O. lineoocellatum*). All three species are all diurnal, give birth to live young and are indigenous to New Zealand (Whitaker, 2000). The northern grass skink is the most widespread skink in Nelson and Marlborough. It typically lives in densely-vegetated grassland or shrub-land from sea level to the subalpine zone (Whitaker, 2000). The northern grass skinks in the Nelson Lakes area are from clade 1b (Liggins et al., 2008). The speckled skink is found in the central North Island, Nelson and Westland (Whitaker, 2000). It is localised and rare within the Nelson/Marlborough Conservancy where it is found on Stephens Island, and at isolated sites at Golden Downs and in the upper Buller catchment (Whitaker, 2000). Speckled skinks typically inhabit densely vegetated grassland, shrub-land or fern-land below 900 m (Whitaker, 2000). The spotted skink is found from Hawkes Bay to south Canterbury (Whitaker, 2000). It is widespread in Nelson and Marlborough east of the Waimea basin (Whitaker, 2000). It inhabits dry scrubby and rocky areas and subalpine grassland to at least 1600 m (Whitaker, 2000). The spotted skink clade from Nelson Lakes area is 1b (Greaves et al., 2007).

The speckled skink is listed on the New Zealand Threat Classification List as at risk, due to being a sparse population in partial decline. Its overall area of occupancy is more than 100,000 ha but this is predicted to decline 10-70% (Hitchmough et al., 2013). It is also listed on the IUCN Red List as near threatened (IUCN, 2015). The spotted skink clade 1b is considered a relic population, with more than 20,000 mature individuals (Hitchmough et al., 2013). However, these populations are sparse and some are in decline (Hitchmough et al., 2013). The northern grass skink clade 1b is not considered threatened, though all species are considered conservation dependant (Hitchmough et al., 2013).

The Rotoiti Nature Recovery Project (RNRP) was established within the Nelson Lakes National Park in 1997 as one of six Department of Conservation 'mainland islands'. In 2001, the control of mustelids expanded into adjacent forest taking the total area to c.5000 ha (Figure 3.1). DOC 200 and 250 traps are used to trap mustelids, and these are spaced 100 m apart. They are checked monthly in winter, fortnightly in spring and autumn and weekly in the summer. Cat and possums are also trapped. A community conservation group, the Friends of Rotoiti (FOR), established in 2001, has increased the effective control area further still, including the habitat of northern grass, speckled and spotted skinks. They set rat traps every 50 m along Ward Street, Black Hill walk and the Black Hill contour as well as in the neighbouring area. They are checked fortnightly.

To monitor the effect of the mammal trapping program on the skink populations, 38 pit-fall traps (Whitaker, 1967) were set in the RNRP in November 2002, coinciding with the onset of mammalian predator-trapping in that area (Figure 3.1). They were divided into two sites, RNRP1 and RNRN2, with 19 pit-fall traps in each (Figure 3.1). The traps were placed along roads and walking tracks.The exact location of each pit-fall trap was chosen based on areas that appeared to be favourable to skinks, thus they were placed in sunny, dry microhabitats. The traps were monitored each summer (November – March) from 2002 to 2012, except for the summer of 2009/2010. For the summers from 2002 to 2009 the traps were monitored over two to five trapping episodes of four days duration. For 2010-2012 monitoring sessions were lengthened to 10 days and were conducted monthly. I collected the data from 2002 – 2007 and 2010-2012, while other FOR volunteers collected the data from 2007 – 2009. When possible trapping was conducted in good weather to maximise catch rates.

I expanded the project in 2010 to investigate long term population trends outside of the RNRP were there is no predator control. I set 50 pit-fall traps at Lake Station in November 2010. The traps were divided evenly into two sites, LSA and LSB, with 25 in each site (Figure 3.1). These traps were spaced evenly within a 20 m^2 grid, with each trap five meters apart. These traps were checked during the same monitoring sessions as the traps within the RNRP. I chose Lake Station because Efford et al. (unpubl. data) conducted a study of the lizard populations there during the summers of 1995 and 1996. Therefore, I was able to compare my results to theirs. They set two grids of 231 pit-fall traps at 5 m spacing baited with canned pear (Efford, 2014a). They checked them over 12 three day intervals (Efford, 2014a). I compared their data from monitoring sessions

six (17 – 20 October 1995) and seven (14-17 November 1995), which are available on R with the library ‘secr’ (Efford, 2014b), with my own data from the summers 2010/2011 and 2011/2012.

The traps set in 2002 were constructed from 3 L canned fruit tins (24 cm x 16 cm). Square tin lids with folded down corners were placed over the top opening. This allowed skinks to crawl in, but kept the rain and sun out. A rock was placed on top to keep the lid on. The pit-falls traps set in 2010 at Lake Station were green 4 L plastic pails. To allow skinks to enter, a gap was created by laying sticks between the pail and the lid. The lid was held in place by a rock. Holes were drilled in the bottom of all pit-falls for water drainage. Each pit-fall trap was placed in the ground such that the top was flush with the soil. The bottom was covered with a thin layer of soil. Traps were then baited with a thumb-nail sized piece of canned pear. To maintain moisture a 7 cm x 5 cm x 0.5 cm kitchen sponge was moistened and placed in the trap. The sponges were washed prior to being used to remove any factory chemicals. On each day of monitoring the old bait was replaced by fresh bait and the sponge moistened. In traps where the sponge dried out within 24 hrs another sponge was added.

When a skink was caught in a trap it was identified, sexed, weighed and measured (snout to vent length; SVL). The skink was then marked on its ventral side with a dot of a silver xylene-free permanent marker pen. A different location for the dot was chosen for each of the 10 days so that the day of capture could be determined on recapture. The dorsal and ventral side of each skink was photographed. It was then released at the point of capture. The above process took around three minutes. For northern grass skinks individuals < 42 mm were considered juvenile (Barwick, 1959; Spencer et al., 1998), while for spotted skinks individuals < 62 mm were considered juvenile (Spencer et al., 1998). On the last day of monitoring the traps were closed by filling them with sticks such that if a skink or other animal fell in it could climb out.

Statistical analyses

Data were analysed using the program R (R Core Team, 2013). The packages ‘gdata’ (Warnes et al., 2013) and ‘lme4’ (Bates et al., 2013) were used. Graphs were created in SPSS 16 (SPSS, 2007) and Grapher 9 (GoldenSoftware, 2011) and edited in Inkscape (Inkscape, 2014). To investigate trends in the northern grass and speckled skink populations between 2002 and 2012 I used linear models with Gaussian distributions. The dependent variable for each model (one for each of the three populations: northern grass skinks RNRP1, northern grass skinks RNRP2,

speckled skinks RNRP2) was captures per trap day, using only the data from the original 38 pit-fall traps. To compare this to the number of mammalian predators killed in the area I plotted the number of rats, mice, stoats, weasels and hedgehogs that were caught in Friends of Rotoiti rat traps and DOC 200 and 250 stoat traps from 2002 – 2012, using the Friends of Rotoiti Rodent Database (Carter, 2013, unpubl. data; DOCDM-917848) and the RNRP Mustelid Database 9812 (Doura, 2012, unpubl. data; DOCDM-1021226). I only used predator trapping data from trapping lines near RNRP1 and RNRP2. Thus, I used the RNRP trapping lines: Peninsula Nature Walk, Anglers Walk, Teatotal Road, Duck Pond, Black Valley Stream and Borlase Boundary, and all of the FOR rat traps. There are too few replicates (10 years) to justify generalised linear model comparisons therefore I graphically assessed the data.

I investigated if the weather changed significantly over the duration of the study in order to evaluate whether changing weather patterns could explain temporal trends in skinks populations. To do this I inspected temporal changes in the: mean daily temperature, mean daily maximum temperature, mean daily minimum temperature, mean daily relative humidity, the proportion of days it rained, the total amount it rained, and the mean amount of precipitation each day it rained. These weather observations were chosen because they are known to influence skink detectability (Hoare et al., 2009). The data were collected from Kawatiri (25 km North West of Saint Arnaud) and obtained from the Meteorological Service of New Zealand Limited. Only the years 2006-2012 were compared because data were unavailable for 2002-2005. Temporal changes in each of the weather observations were tested for by running a linear model for each observation over the six year period.

Results

Long term population study (2002 – 2012)

In total I captured 767 northern grass skinks, 76 speckled skinks (71 RNRP2, 5 Lake Station, 1 RNRP1) and 16 spotted skinks (5 from RNRP2; all prior to 2008 and 11 from Lake Station). Over the decade from November 2002 – March 2012, the number of skinks captured per trap day decreased, for both northern grass and speckled skinks, and for both trap lines (RNRP1 and RNRP2; Figure 3.2). Only one speckled skink was caught during each of the 2010/2011 and 2011/2012 summers. The declining trend was strongest for the RNRP1 northern grass skink

population (slope = -0.014, t = -3.75, df_7, P = 0.0072, R^2 = 0.62; Figure 3.2), followed by the RNRP2 speckled skink population (slope = -0.008, t = -3.25, df_7, P = 0.014, R^2 = 0.54; Figure 3.2) and lastly the RNRP2 northern grass skink population (slope = -0.006, t = -3.44, df_7, P = 0.011, R^2 = 0.58; Figure 3.2). The northern grass skink RNRP1 population was declining faster than the northern grass skink RNRP2 population (F = 9.88, $df_{5,21}$, P = 0.047). There was no significant difference between the slope of the decline in the northern grass skink and speckled skink RNRP2 populations (F = 9.88, $df_{5,21}$, P = 0.54) or the northern grass skink RNRP1 population and speckled skink RNRP2 population (F = 9.88, $df_{5,21}$, P = 0.15). Northern grass skinks were caught in both areas while only one speckled skink was caught at RNRP1.

The number of mammalian predators caught in Friends of Rotoiti rat traps and Department of Conservation DOC 200 & 250 stoat traps do not show any overall trends between 2002 and 2012 (Figure 3.3). Hedgehogs were the only species showing a strongly decreasing trend (Figure 3.3). Stoats showed yearly fluctuations with no overall increasing or decreasing pattern in catch rate (Figure 3.3). The weasel catch rate was similar across years, except for a peak in 2009, corresponding with a mast year (Figure 3.3). The number of mice caught fluctuated greatly with a spike in 2009, again corresponding with the mast year (Figure 3.3). The rat and cat catch rates were similar across this period (Figure 3.3), while the ferret catch rate showed a slight decreasing trend (Figure 3.3).

From 2002 – 2010 the weasel and northern grass skink catch rate show a predator – prey style relationship with increases in weasel catches being reflected by decreases in skink catch rate and vice versa (Figure 3.4). A similar pattern was seen with hedgehogs (Figure 3.5) and stoats (Figure 3.4) in respect to northern grass skinks. From 2002 – 2006 northern grass skinks and ferrets showed a similar predator-prey pattern, but from 2006 onwards the two populations both decreased substantially and showed similar fluctuations as opposed to a predator-prey style relationship (Figure 3.4). There was no strong pattern present between cats, rats or mice killed and northern grass skink captures (Figures 3.4 & 3.5). There was no apparent relationship between the catch rate of speckled skinks and any predator (Figures 3.4 & 3.5).

Recruitment

Sustained predator control in the RNRP over the duration of my study would be expected to lead to increased rates of recruitment. For northern grass skinks (Figure 3.6) there was no apparent change in the recruitment portfolio for the population between 2002 and 2012. A wide age (size) range from young to old was present throughout (Figures 3.6). In the speckled skink population, the younger (smaller) skinks appeared to have disappeared from the population (Figure 3.7). From the summer of 2006/2007 onwards, no skinks < 50 mm were captured. In addition, no individuals under 40 mm were ever captured (Figure 3.7), suggesting recruitment is very low.

Lake Station, a comparison with 1995

In all species the catch per trap day has decreased (Table 3.1). This is most apparent for speckled and spotted skinks (Table 3.1). The species composition has changed dramatically; in 1995 speckled skinks were the most prevalent species, followed by spotted skinks (Table 3.1). In 2010-2012, northern grass skinks were the most common species, with some spotted and few speckled skinks being caught (Table 3.1).

Weather

None of the weather variables tested (mean daily temperature, mean daily maximum temperature, mean daily minimum temperature, mean daily relative humidity, the proportion of days it rained, the total amount it rained, and the mean amount of precipitation each day it rained) changed significantly between 2006 and 2012 (Table 3.2).

Discussion

Mammalian predator control and skink abundance

The decrease I observed in the skink populations within the RNRP over the past decade is probably due to the mammalian predators not being reduced enough to allow the skink populations to stabilise or recover. This is supported by my findings that the number of mammals trapped inside the RNRP in the area of my study has not decreased significantly. The decline in catch rate of skinks over the decade of monitoring is parallel to the decline in catch rate seen at Lake Station between 1995 and 2010-2012. Similar to within the RNRP, the sharpest decline was seen in the larger and rarer species (speckled and spotted skinks). A similar pattern has been seen in the Pukerua Bay lizard population (Hoare et al., 2007a). The skink populations in this areas

are also in decline, with the larger bodied species decreasing the fastest (Hoare et al., 2007a). This is also probably due to predation by mammalian predators (Hoare et al., 2007a).

A similar lack of effectiveness of low to medium intensity predator control has been seen in other studies (Reardon et al., 2012; Wilson, 2007) . A predator control regime was implemented to protect the critically endangered grand skink (*Oligosoma grande*) and the Otago skink (*O. otagense*). There were three levels of treatment: 1) near-eradication inside a mammal proof fence; 2) suppression of mammal by trapping within 21,00 ha area; and 3) unmanaged predator population. For northern grass skinks, and other small lizard species (McCanns skink [*Oligosoma maccanni*], cryptic skink [*O. inconspicuum*] and common gecko [*Woodworthia maculate*]) the only significant increase in lizard populations was within the predator proof fence (Wilson, 2007). Trapping predators alone was not enough to significantly increase the skink population compared to the control area (Wilson, 2007). A similar pattern was seen in the grand and Otago skink populations (Reardon et al., 2012). Both these skink populations increased the most within the mammal-proof fence and in the centre of the predator-trapping treatment (Reardon et al., 2012). However, survival was significantly higher within the mammal-proof fence than in the trapping area (Reardon et al., 2012). In the unmanaged areas, the grand skink population declined dramatically while the Otago skink population was stable (Reardon et al., 2012). For grand skinks there was little or no change in the population size at the trapping periphery (Reardon et al., 2012). Therefore, a similar situation may be happening with the skinks within the RNRP because the skink population that I was studying is located near the edge of the mammal control area (~ 1000 m), where predation may not be reduced to a great enough extent.

Complete eradication of mammalian predators from islands has resulted in substantial increases in lizard and tuatara populations (Towns, 1991; Towns et al., 2001). Following the removal of rats there was an increase in the capture frequency of speckled skinks on Moutohara Island (Towns et al., 2002) and Mokoia Island (Owen, 1997). Likewise, spotted skinks on Matuia/Somes Island also increased after mammalian predator removal (Neill, 1997). Reintroductions of lizards to islands post predator removal have been very successful, suggesting that it was the presence of predatory mammals (primarily rats) rather than habitat or other factors that caused these species to be absent from the island (Towns, 1991; Towns and Daugherty, 1994; Towns and Ferreira, 2001). This shows that skink populations can rebound following

substantial reductions in mammalian predator populations. Thus, the fact that this has not been seen within the RNRP suggests that the predator population has not been decreased to a level to allow the skink populations to stabilise or increase.

Recruitment

The considerable decrease in number of younger speckled skinks implies that either the speckled skinks are not producing offspring or that most of the young are being eaten in preference to larger individuals. I never caught a speckled skink less than 40 mm SVL, and the last juvenile (< 55 mm SVL; Chapter 2) was caught in 2005. This has serious implications for the viability of this population. It has been in steady decline since monitoring began and has dropped to almost nil, with only one individual caught in the summer of 2010/2011 and one in 2011/2012. This is similar to other lizard recruitment trends. Kiore appear to limit recruitment into Duvaucel's gecko (*Hoplodactylus duvaucelii*) populations (Hoare et al., 2007c). On Ōhīnau island, where kiore have been present up until 2005, the Duvaucel's gecko population was skewed towards larger individuals compared to the mammalian predator-free Korapuki and Green Islands (Hoare et al., 2007c).

Intervention appears necessary to stop the speckled skink population from becoming locally extinct. Mammalian predator control should be increased, targeting all species as it is not clear which predator is currently the most damaging. In addition, research is urgently needed to determine whether the population is reproducing or why are the young dying. Reintroductions of speckled skinks from large, stable or increasing populations may be necessary. The population has become so small it may not be able to recover without additional individuals due to Allee effects. Regardless of the steady population decrease there has been no apparent change in the recruitment portfolio in the northern grass skink population. Thus, the population is still breeding successfully and predators do not appear to be selecting one size class.

Mammalian predator and skink population dynamics

From 2002 – 2010 the trapping rate of weasels, hedgehogs and cats show a possible predator – prey style relationship with the northern grass skink catch rates. Increases in weasel, hedgehog and cat catch were reflected by decreases in skink catch rate and vice versa. This suggests that these three species may be primarily responsible for the decline in the skink population although

further data over a longer term frame is needed to confirm this pattern. The lack of a correlation between skink and the trapping rates of the other mammalian predator species does not necessarily mean these predators are not also involved in skink population declines. In fact, any evidence of a predator prey style relationships is surprising given the complexity of the ecological interactions in my study system and the relatively short duration of my study. There are four main reasons for this. Firstly, it has been shown (Reardon et al., 2012; Wilson, 2007) that even reduced densities of mammalian predators can lead to continued lizard population declines. The catch rate of mammalian predators in the RNRP over the course of my study indicates there are still plenty of predators present. Secondly, some of the predators such as stoats and rats showed little fluctuation in the numbers trapped per year, thus a statistical correlation is not expected between these catch rates and those of the skinks, even though they are probably eating skinks. Statistical correlations will only be seen when the predator populations fluctuate significantly enough for the differences to be seen in the skink populations. Thirdly, since the catch rates of the predators do not all fluctuate in synchrony with each other (due to predation between predators species, competition and different food sources, etc.) any differences seen in the skink population from a decrease in the presence of one predator species may be masked due to the increase in predation from another predator species or vice versa. Fourthly, it can take decades to see patterns between predators and prey populations (Elton and Nicholson, 1942). A lack of any obvious predator-prey relationship between the speckled skink population and any mammalian predator species is probably due to the strong decreasing trend and low catch rate of speckled skinks. It appears the level or predation was high enough at all times that the population was never able to rebound following a decline on any predator species.

Natural events such as beech masting may lead to increased levels of predators due to an amplified rodent population in response to the increased food available, which in turn creates a corresponding response in the mustelid populations (as seen in the mouse and weasel populations during the 2009 mast). When the mast is over, these predators need to seek an alternative food source and may turn to birds, lizards and other endemic fauna (King, 1983; Wilson and Lee, 2010). The skink population did not appear to decrease at a faster rate after the mast year, suggesting mice and weasels may not be their most significant predators. This further suggests that hedgehogs and cats may be the most significant predators of these skinks.

Lake Station, a comparison with 1995

In all species the catch per trap day at Lake Station has decreased between 1995 and my study, with the greatest decline seen in speckled and spotted skinks**.** The species composition has also changed dramatically. In 1995 speckled skinks were the most prevalent species, followed by spotted skinks. In 2010-2012 northern grass skinks were the most abundant species with some spotted and few speckled skinks being caught. It is important to note that speckled skinks are known to be more trappable than spotted skinks (Efford *et al*., unpubl. data), thus the proportion of species in the community may be different to proportions caught. Regardless, it is unlikely that trappability changes over time, thus as a temporal comparison the changes in species composition are relevant. As my methods were very similar to those of Efford et al. (unpubl. data) differing trapping methods are not a probable explanation for the differences between years. In addition to the general decline in catch rate, since the 1970's (Spencer et al., 1998) the proportion of female northern grass skinks caught at Lake Station has decreased, as well as larger individuals of both sexes (Chapter 2). A hypothesis for this is that females and larger individuals are more vulnerable to predation by introduced mammals (Chapter 2).

I suggest continued monitoring of this skink community as all species appear to be in decline. The reason for decline is unknown, but may be due to: fire, removal of individuals or predation. The grass and bracken hillside where the skinks are found is not grazed, but is burnt every 7-10 years (Ingrid McConochie, *pers. comm*., 2014). The effects of this burn regime are unknown. It may benefit the skinks by stopping reforestation and thus maintaining the vegetation type. Alternatively, the fire may kill skinks, and/or indirectly cause detrimental effects on the population by pushing them into the surrounding grazed grassland that has little cover or food, and therefore increasing the probability of mortality through predation and starvation. In 1995 skinks were removed from the site as part of a research project (Bruce Thomas, *pers. comm*., 2015). In addition, a very hot fire burnt the site in the same year (Bruce Thomas, *pers. comm*., 2015). These events, in combination with the continuous predation pressure, may be the cause of the observed decline.

I recommend further investigation into the reason for the skink population decline at Lake Station and potential conservation measures. The preservation of spotted and speckled skink populations at Lake Station is crucial for the continued preservation of these species in the St.

Arnaud area; especially as it is the only location they were found other than RNRP2, where they are also in decline. Northern grass skinks may be surviving better than speckled or spotted skinks because they are smaller and known to co-exist better with mammalian predators (Hitchmough et al., 2013). The presence of juvenile spotted skinks is reassuring (Chapter 2), as it indicates the species is breeding successfully, though it appears few are making it to adulthood.

Alternative hypotheses for the decrease in skink abundance

Other potential explanations for the decrease in the skink populations within the RNRP over the past decade are: competition with mammals for food, predator release of natural avian predators such as weka, kingfisher and falcons, changing habitat and changing climate. The mammals may be competing with the skinks for food as they have similar diets (McCallum, 1986; Whitaker, 1978). For example, invertebrates, which are eaten by reptiles, are also important in the diet of rodents and hedgehogs in New Zealand (Best, 1969; Bettesworth and Anderson, 1972; Daniel, 1973; Jones et al., 2005; Spitzen-van der Sluijs et al., 2009). Likewise, kiore have been reported to have negative effects on invertebrate populations, including that of terrestrial snails, flightless crickets, beetles, earwigs and spiders (Towns, 2009), and this could be true for other rat species. In addition, ship rats have been found to eat soft fruits (Daniel, 1973), which are important in the diet of some lizards (Freeman, 1997; Olesen and Valido, 2003; Patterson, 1992; Spencer et al., 1998). Northern grass and speckled skinks have been found to eat a wide range of prey including Coleoptera, Araneae, Lepidoptera larvae, Orthoptera, Diptera, Hemiptera, arthropod eggs and fruits such as that from the native shrub *Leucopogon*sp and blackberry (*Rubus fructicosus*) (Efford et al., 1997; Freeman, 1997; Patterson, 1992; Spencer et al., 1998). Speckled skinks are suspected to have a similar diet. Thus, a high rodent and hedgehog population may be decreasing the food available to skinks, putting increased pressure on their populations. Assessing food availability was beyond the scope of this study, but it would be worth investigating.

It is possible that the bird populations are rebounding better in response to the mammalian predator control than the skink populations, thus increasing predation on the skinks. The population trends of predatory birds since the creation of the RNRP have not been recorded and therefore I was unable to investigate this theory. RNRP2 was burnt in the 1930's and is thus in the process of regeneration, so there has been a change in the habitat over the duration of the

study as the forest matures. This has potentially decreased the habitat available for skinks, though it still appears to be good as there is open mānuka and braken with rocky outcroppings. There has been little change in habitat along RNRP1 over the past decade, thus this is not a likely explanation for the decrease seen in this population. There appears to have been no long term changes in the weather, therefore it is also an improbable reason for the skink decline. Another possible, but unlikely explanation is that the decrease in catch rate is due to the skinks becoming trap shy. This is quite unlikely given that other studies have observed populations being stable or increasing over long periods of time (Hoare et al., 2007a; Lettink et al., 2011).

Conclusion

A long-term study of the skink populations in the RNRP demonstrated that the current level of mammalian predator control occurring is insufficient to protect or to allow for the recovery of the indigenous skink populations. The northern grass and speckled skink populations within the RNRP have decreased significantly between 2002 and 2012, with the speckled population near local extinction. Throughout the study period, northern grass skinks showed a stable recruitment portfolio. In contrast, the number of younger speckled skinks has decreased over the decade, potentially decreasing the population's viability. Other potential explanations for the decrease in the skink populations within the RNRP over the decade include: food competition between skinks and mammals, an increase in natural predators and habitat change. Nevertheless, these factors seem unlikely compared to the pressure of mammalian predation. A parallel decline in skink catch rate is seen outside of the RNRP at Lake Station. Between 1995 and 2010-2012 the catch rate of all species has decreased, with the sharpest decline seen in the rarer species. This decline of populations throughout the area highlights the importance of lizard conservation as without human intervention these populations, especially those of speckled and spotted skinks, may be at risk of local extinction.

To design effective species management systems it is important to know to what level predators need to be reduced to allow species recovery (Sinclair et al., 1998). It appears this has not been reached with the RNRP. Skinks are not the mammalian predators primary food source, therefore the *per capita* predation rate on the skinks most likely increases as skink density declines (Sinclair et al., 1998). Therefore, predators may need to be reduced to a very low abundance to

allow the skink populations to increase. The RNRP is designed to protect birds within the beech forest, and therefore this is where most of the mammalian trapping takes place. Skinks do not live in beech forest; they prefer the sunny shrub and grass clearings. Thus these areas, and the surrounding areas, need to have increased mammalian predator control to reduce predator numbers to a level where the skink populations can rebound. Past research has shown that predator control can be successful in allowing skink population recovery. Increasing survival and/or reproduction rates of skinks, through habitat manipulation, increased food or refuge sources, etc., may prove an alternative strategy. It could allow skink populations to increase without needing to decrease predator numbers to as great an extent (Sinclair et al., 1998; Souter et al., 2004). However, to date this has not proved successful in New Zealand (Lettink et al., 2010), and control of mammalian predators is likely to be the key factor in ensuring the survival of skinks over the long-term.

Figures and Tables

Table 3.1: A comparison of skink populations at Lake Station between 1995 (Efford et al., unpubl. data) and 2010-2012. Capture per trap day does not include recaptures.

	1995	2010-2012
Species	**Captures per trap day**	**Captures per trap day**
Northern grass	0.026	0.014
Speckled	0.116	0.001
Spotted	0.045	0.003

Table 3.2: Linear model outputs to investigate changes in weather from 2006 – 2012.

Observation	**Slope**	**R^2**	**Standard error**	***t* value**	***P* value**
Mean daily temperature (°C)	0.02	0.02	0.06	0.30	0.78
Mean daily maximum temperature (°C)	-0.09	0.11	0.11	-0.80	0.46
Mean daily minimum temperature (°C)	0.05	0.11	0.06	0.79	0.46
Mean daily relative humidity (%)	0.25	0.15	0.27	0.95	0.39
Total rain (mm)	-0.10	0.00	38.94	0.00	1.00
Proportion of days it rained	0.00	0.01	0.01	0.26	0.81
Mean rain per rain day (mm)	-0.05	0.02	0.14	-0.33	0.75

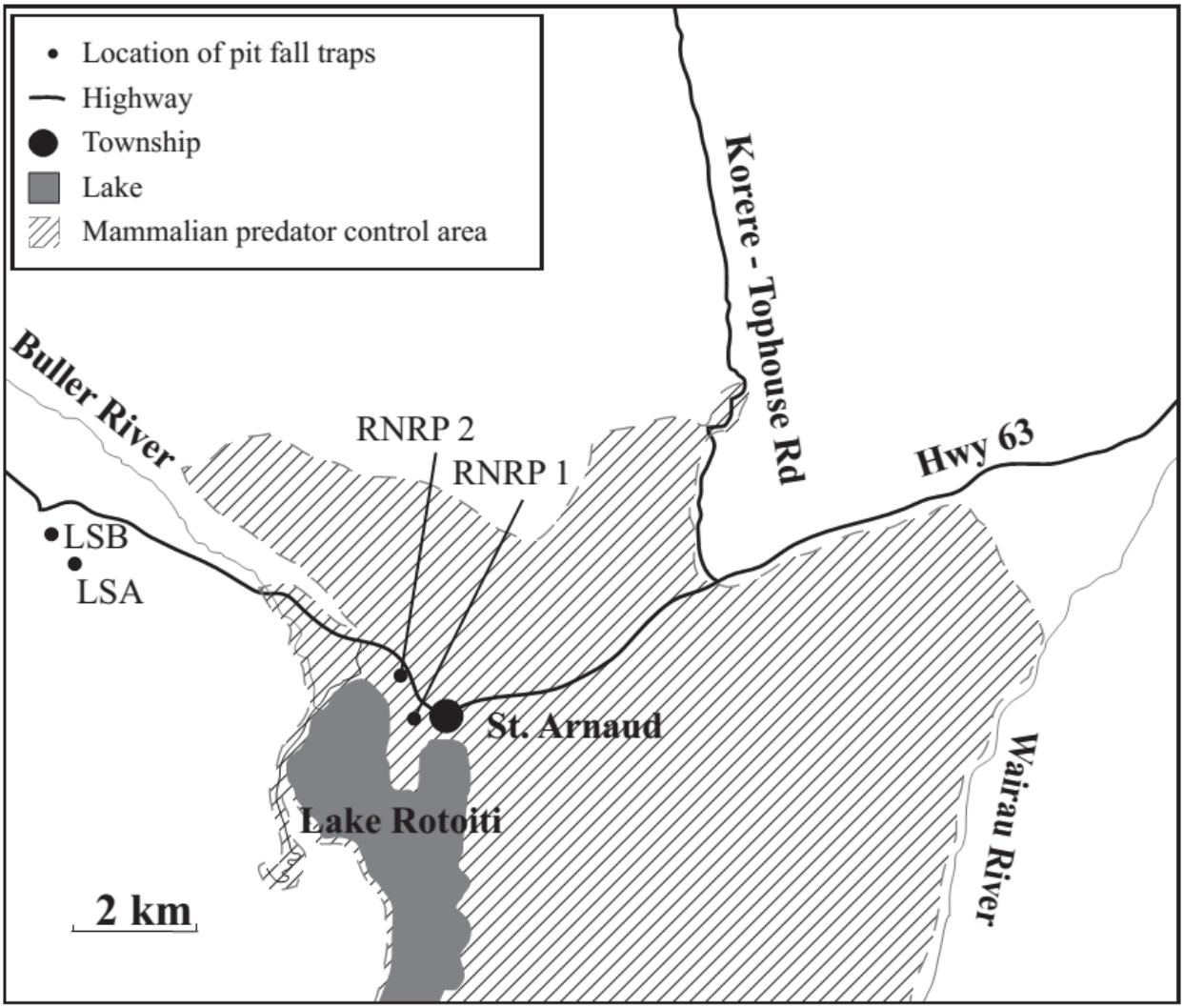

Figure 3.1: Map of the St. Arnaud area, location of skink pit-fall traps and the mammalian predator control area.

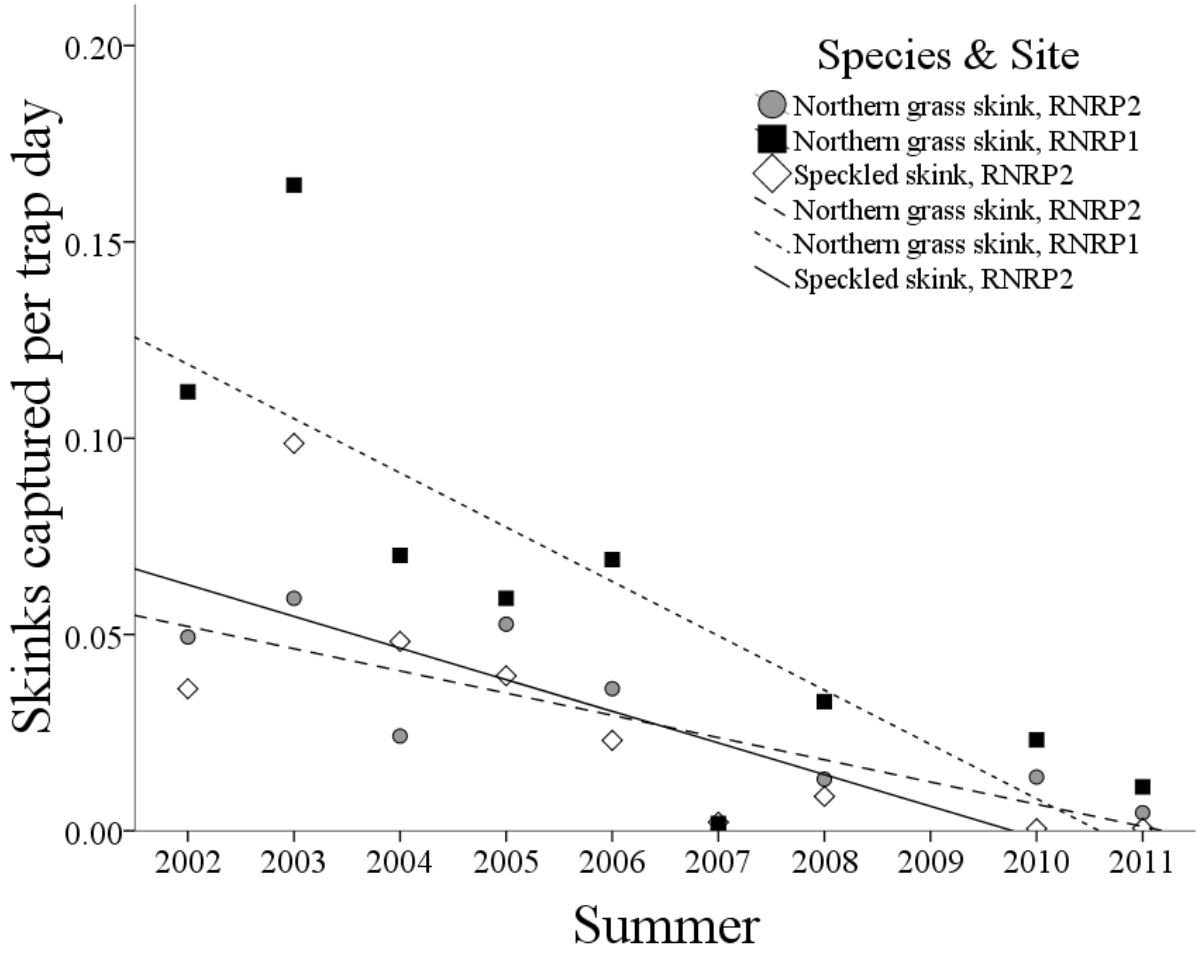

Figure 3.2: The number of northern grass and speckled skinks captured in the RNRP1 and RNRP2 pit-fall traps, per trap day, between November 2002 and March 2012. Linear trend lines shown. 'Summer' refers to the year that the summer begins, e.g. '2002' refers to November 2002 – March 2003 and '2003' refers to November 2003 – March 2004.

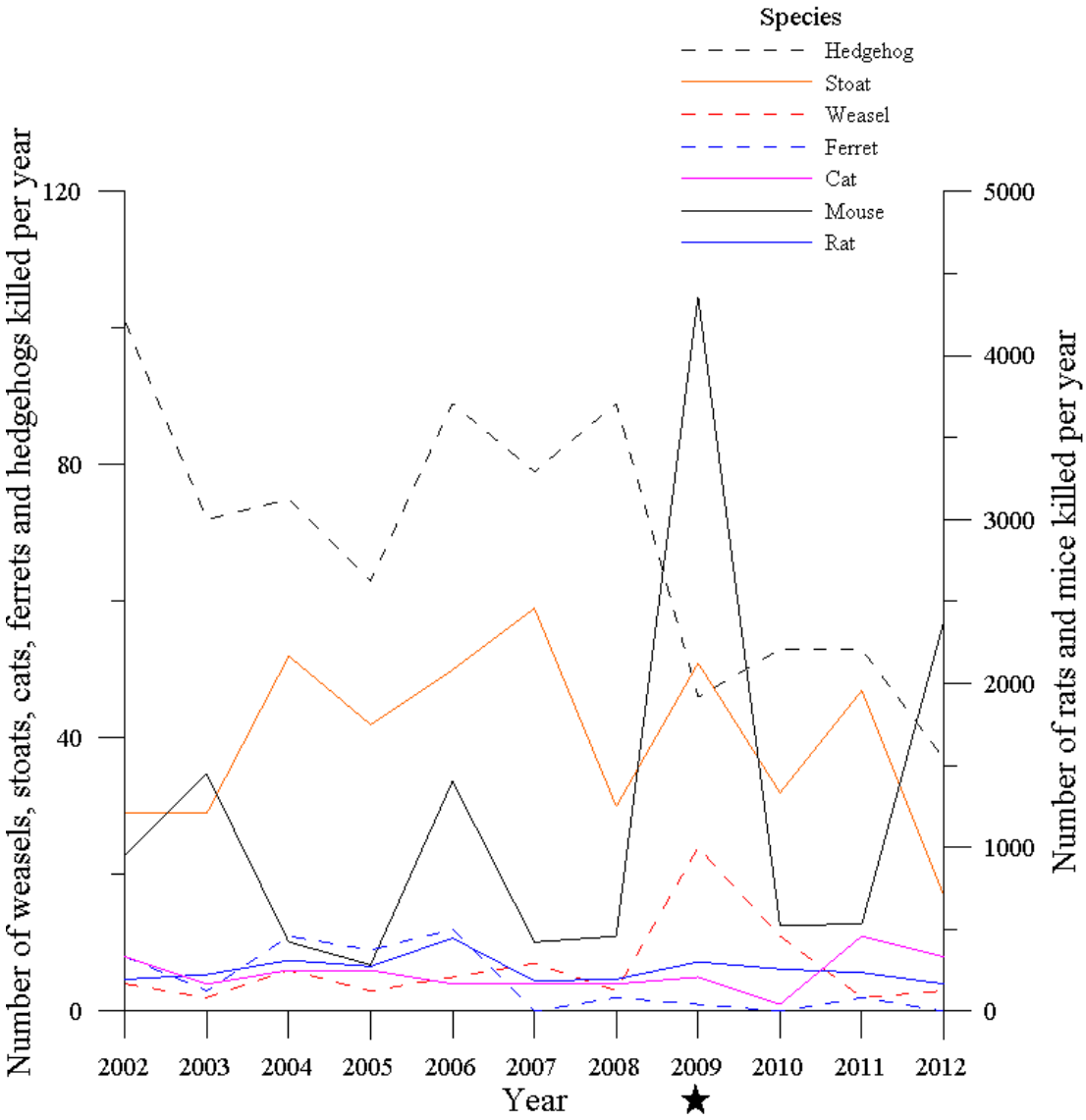

Figure 3.3: The number mammalian predators trapped near RNRP1 and RNRP2, between 2001 and 2012. 'Year' refers to the year that the financial year (1 July – 30 June) begins, e.g. '2002' refers to 1 July 2002 - 30 June 2003. Star indicates mast year (2009).

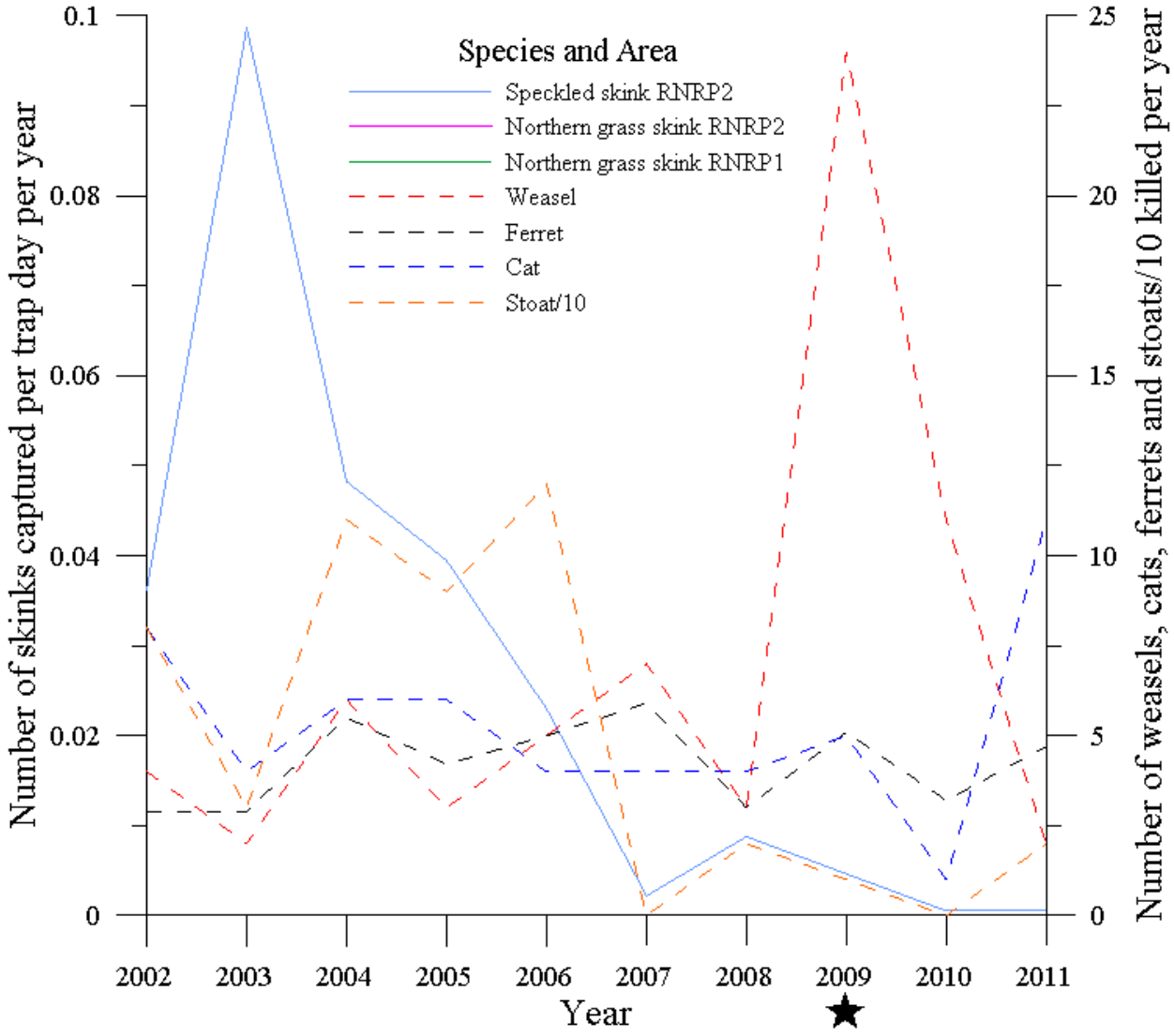

Figure 3.4: A comparison between the number of northern grass and speckled skinks caught in RNRP1 and RNRP2 each year in relation to the number of weasels, cats stoats and ferrets trapped each year near RNRP1 and RNRP2 between 2001 and 2012. The number of stoats killed per year is divided by 10 to fit the scale. 'Year' for the mammalian predator data refers to the period from 1 July – 30 June (e.g. '2002' refers to 1 July 2002 - 30 June 2003). 'Year' for the skink data refers to the year that the summer begins, e.g. '2002' refers to November 2002 – March 2003. Star indicates mast year (2009).

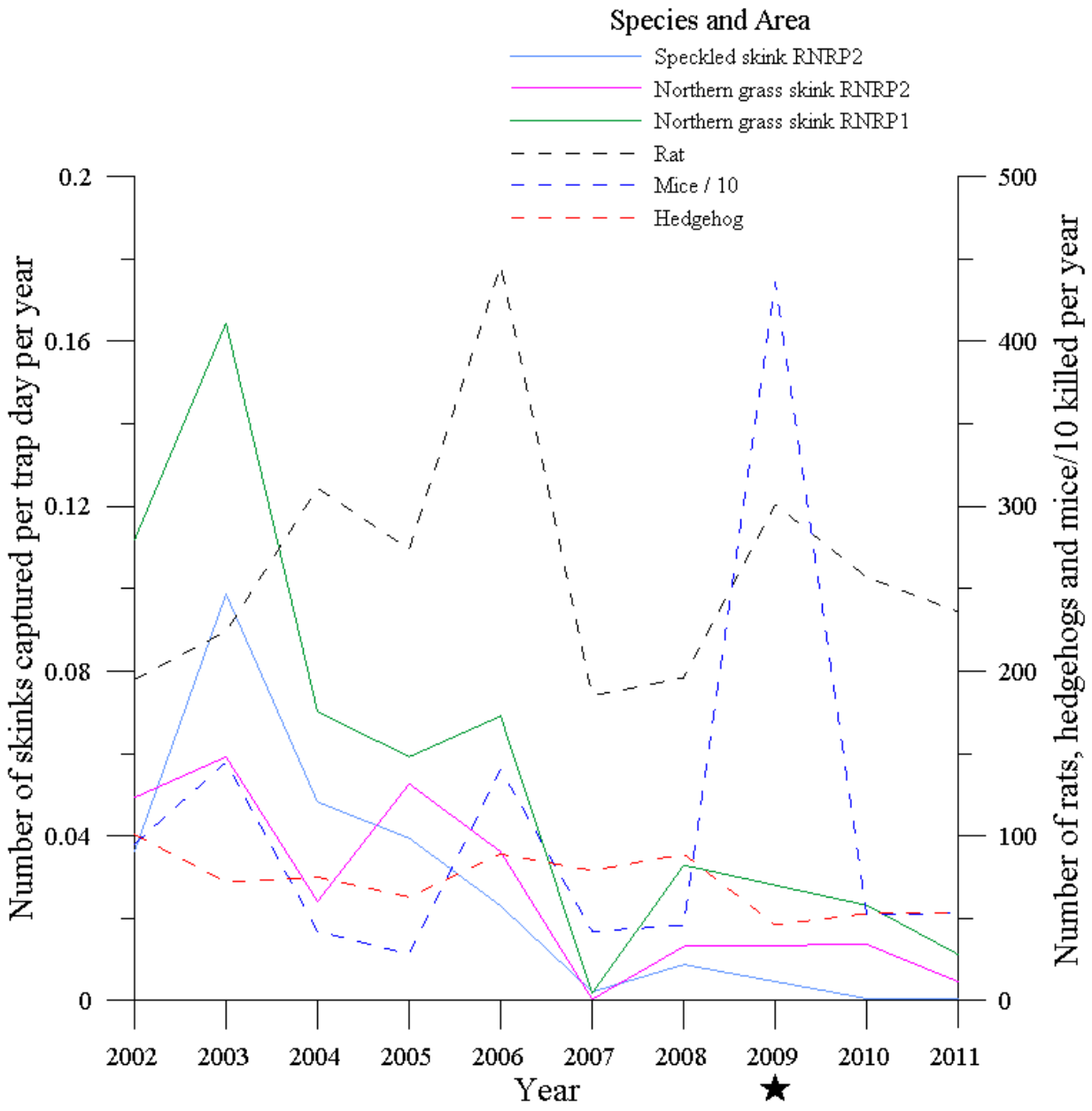

Figure 3.5: A comparison between the number of northern grass and speckled skinks caught in RNRP1 and RNRP2 each year in relation to the number of rats, hedgehogs and mice trapped each year near RNRP1 and RNRP2 between 2001 and 2012. The number of mice killed per year is divided by 10 to fit the scale. 'Year' for the mammalian predator data refers to the period from 1 July – 30 June (e.g. '2002' refers to 1 July 2002 - 30 June 2003). 'Year' for the skink data refers to the year that the summer begins, e.g. '2002' refers to November 2002 – March 2003. Star indicates mast year (2009).

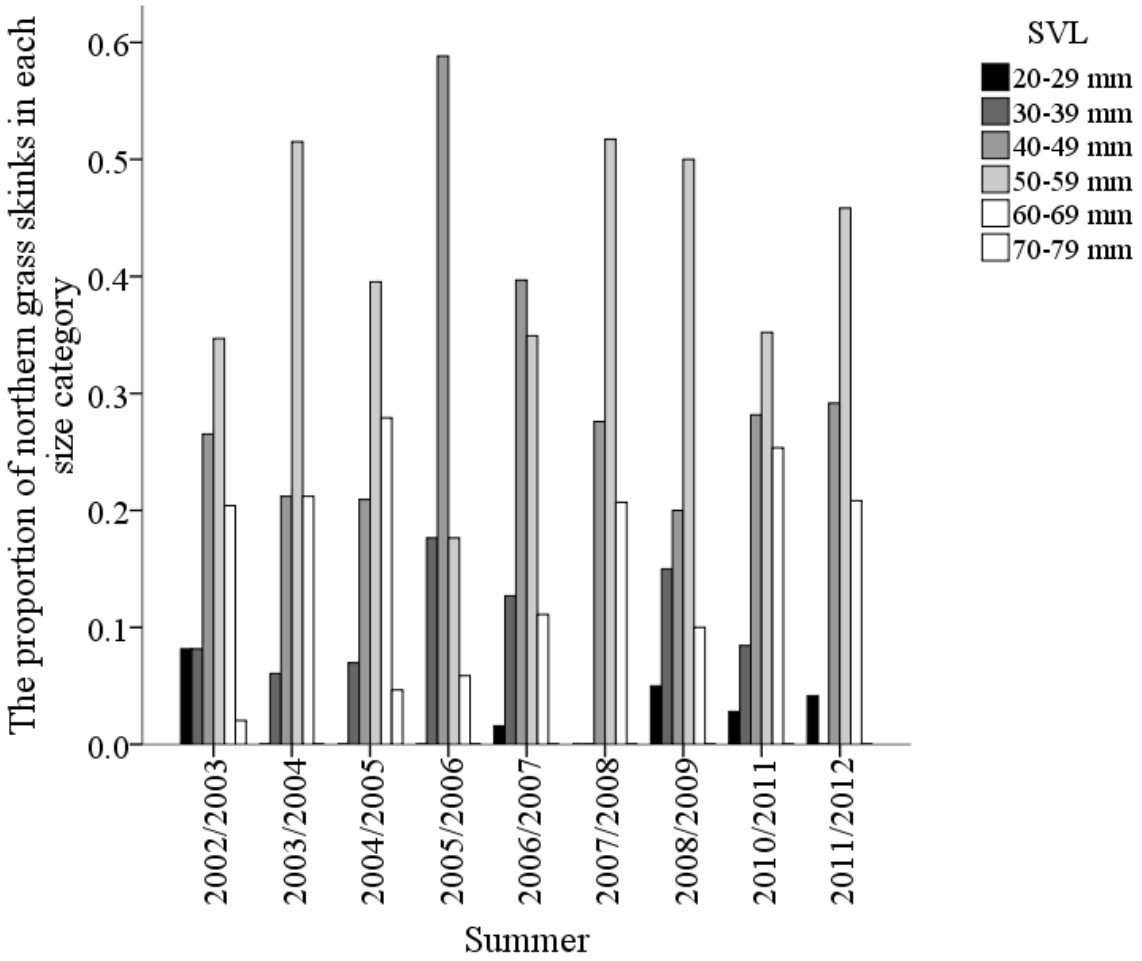

Figure 3.6: The proportion of northern grass skinks in each size category over each summer (RNRP1 and RNRP2).

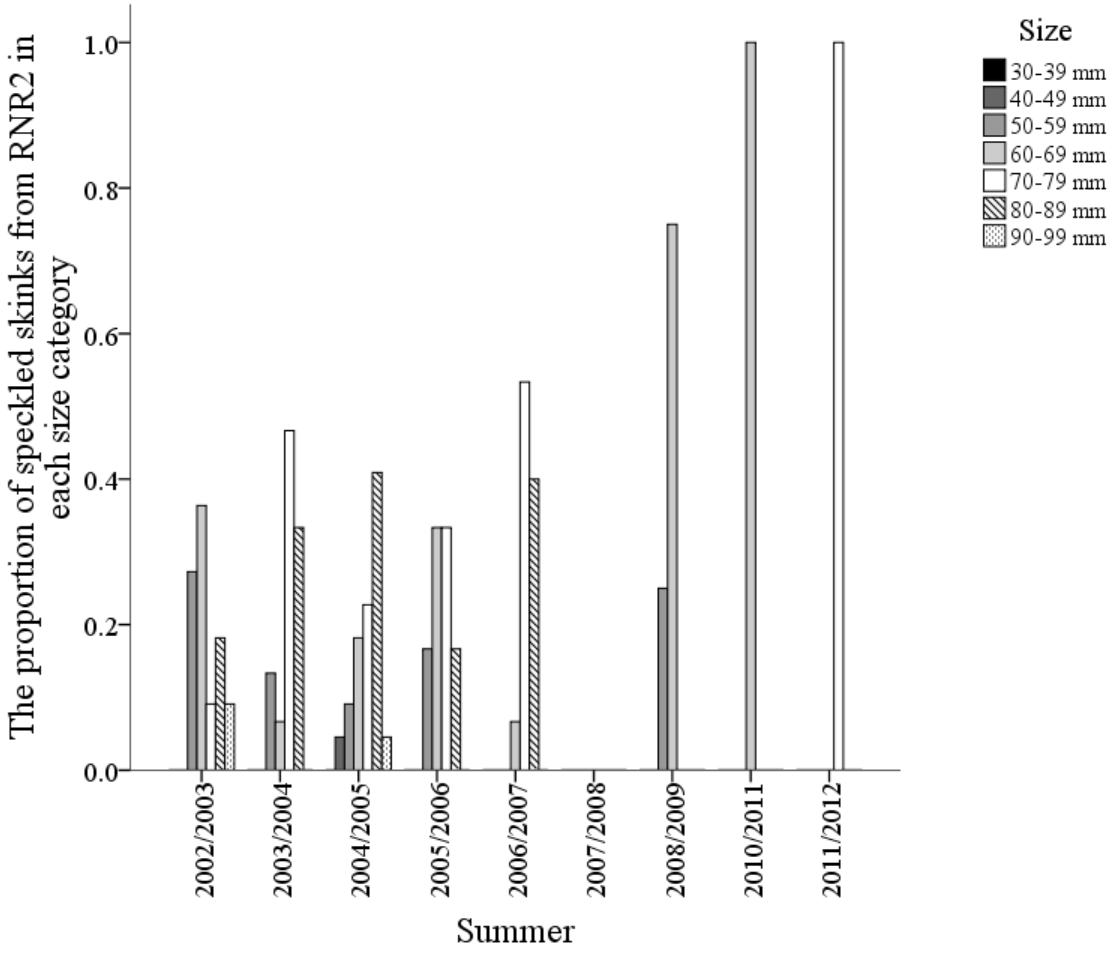

Figure 3.7: The proportion of speckled skinks from RNRP2 in each size category over each summer.

Chapter 4: The importance of sub-lethal predation: introduced mammalian predators cause a decline in the body condition of native skinks

Abstract

Avoiding predation can come at the cost of other activities such as foraging and maintenance behaviours. Though often overshadowed by the lethal aspects of predation, non-lethal effects of predators can have a significant influence on the fitness of individuals and populations. I investigated three possible effects of sub-lethal predation: body condition, caudal autotomy, and parasite load in two species of New Zealand skink (northern grass skink *Oligosoma polychroma* and glossy brown skink *O. zelandicum*). I compared populations with and without the presence of introduced mammalian predators. For both species body condition was lower in populations with mammalian predators present. In addition, for northern grass skinks in areas with mammalian predators present, skinks with caudal autotomy had higher body condition than those without. Unexpectedly, caudal autotomy was more common in the absence of mammalian predators, perhaps due to increased antagonistic intraspecific interactions of skinks at higher density in the absence of mammals, or because such sites had more native predators that hunt during the day and are therefore more likely to grab a skink by the tail. The presence of mammalian predators had little effect on the load of parasitic chigger mites. This research suggests that introduced mammalian predators may be causing significant sub-lethal effects on native lizards. This has serious conservation implications because it shows that lizard populations may not only be in decline from direct predation, but also from the additional stresses associated with that predation. This may lead to reduced reproductive output. In addition, the complex interactions between body condition, caudal autotomy, sex and species highlights that different species, sexes, and size classes/body conditions within species, may be experiencing dissimilar predation pressure.

Introduction

Since the arrival of humans and invasive mammalian predators, New Zealand has lost two lizard species (Daugherty et al., 1994) and many of the surviving species have restricted distributions (Bull and Whitaker, 1975; Towns and Daugherty, 1994; Worthy, 1987c). Currently, 37% of New Zealand's lizard species are restricted to offshore islands which were never reached by introduced mammalian predators, or from which these predators were removed (Towns et al., 2001; Worthy, 1987b). As there is no evidence of range reduction in reptiles prior to the arrival of humans in New Zealand, this suggests that introduced predators have been responsible for the decline (Towns and Daugherty, 1994). In contrast, reptiles in countries that coevolved with mammalian predators have been found to be less susceptible to novel mammalian predators (Gibbon et al., 2000).The New Zealand Threat Classification System lists 32 species of reptiles as threatened and another 50 as at risk (Hitchmough et al., 2013). Many species are also listed as threatened globally (IUCN, 2015).

Although there are many examples of the lethal effects of mammalian predators on New Zealand's indigenous lizards, non-lethal predation effects are not well understood. Though often overshadowed by the lethal aspects of predation, non-lethal effects of predators can have a significant influence on populations and ecosystems (Lima, 1998a). In the presence of predators, prey may change their behaviour to avoid being preyed upon (Kotler et al., 1991; Lima, 1998b). These changes can come at the cost of other activities such as feeding and finding mates (Lima and Dill, 1990; Sih, 1987). The immediate cost of increased anti-predator behaviour is lowered energy intake (Lima, 1998a). Over time this can lead to decreased body condition and thus lowered fitness (the number of fertile offspring an individual produces; Lima, 1998a). Reduced fitness of individuals can in turn significantly reduce population size. As it is difficult to directly measure the fitness of individuals, surrogates of fitness are often used. These are easily measureable traits that are known to correlate with individual fitness (Lima, 1998a).

In this study I investigated three possible fitness surrogates of the effects of sub-lethal predation; body condition, caudal autotomy and parasite load, in two skink species (northern grass skink *Oligosoma polychroma* and glossy brown skink *O. zelandicum*) with differing levels of mammalian predation. I hypothesised that there would be decreased body condition, a higher frequency of caudal autotomy and a greater parasite load in the skink populations sympatric with

mammalian predators than populations of the same species on offshore islands without mammalian predators. Differences between skinks that are related to their different risks of predation would indicate that mammalian predators can cause significant sub-lethal effects (in addition to lethal effects) that could lead to reduced population growth.

Body condition is a measure of body mass that takes into account body size. It is intimately linked to an organism's health (Peig and Green, 2009) and has been widely used as a determinant of fitness (Peig and Green, 2010). A decrease in body condition can have consequences for the short and long-term fitness of individuals. In lizards it can lead to decreased fitness as the amount of stored fat affects survival and reproductive success (Andren and Nilson, 1983; Ballinger, 1977; Civantos and Forsman, 2000; Civantos et al., 1999; Ferguson and Fox, 1984; Hoare et al., 2006; Laurie and Brown, 1990; Pond, 1981). Prey often respond to increased predation risk by increasing refuge use (Martín and López, 1999a, b; Sih et al., 1992), which in lizards may decrease body condition due to reduced time spent foraging and thermoregulating (Amo et al., 2007b; Martín and López, 1999a). Reduced food intake can lead to decreased size and survival (Le Galliard et al., 2005) and lost opportunities for thermoregulation can impact on the processing and digestion of food (Autumn and De Nardo, 1995; Avery, 1984; Harwood, 1979). Fleeing at high speed is also a costly antipredator behaviour (Amo et al., 2007a; Christian et al., 1997; Gleeson and Hancock, 2002). In juvenile large psammodromus (*Psammodromus algirus*), increased predator attacks resulted in lower rates of growth and mass gain (Civantos et al., 2010). Similarly, in both the lizard *Iberolacerta cyreni* and the common wall lizard (*Podarcis muralis*), individuals had lowered body condition in populations with greater perceived predation pressure; it is thought this was caused by more time spent in antipredator behaviours (Amo et al., 2006; Amo et al., 2007a). A similar pattern has also been demonstrated in Duvaucel's geckos (*Hoplodactylus duvaucelli*) in New Zealand (Christmas, 1995). On rat-free islands, this species was found to weigh more than individuals on rat-inhabited islands (Christmas, 1995). In contrast, the body-tail condition of the Chevron skink (*Oligosoma homalonotum*) was not found to change significantly between sites with and without rat control (Barr, 2009).

Sacrificing body parts to escape predators or in antagonistic encounters with conspecifics is known as autotomy (Bateman and Fleming, 2009; Maginnis, 2006). Caudal autotomy (tail loss) to escape predators is widespread in lizards (Arnold, 1984; Bellairs and Bryant, 1985; Congdon

et al., 1974), and has been observed in 13 of the ~20 lizard families, including New Zealand skinks (Downes and Shine, 2001). Caudal autotomy can benefit an individual by allowing it to escape a predator that has caught them by the tail, or by creating a distraction as the tail will often twitch after it is shed, which captures the attention of the predator while the lizard escapes (Arnold, 1984). The immediate benefit of caudal autotomy is obvious, but tail loss can also incur costs. Autotomy can increase risk of infection (Arnold, 1984) and over the long term, it can reduce energy stores (Avery, 1970; Congdon et al., 1974; Maiorana, 1977; Smyth, 1974; Vitt and Cooper Jr, 1986), slow growth (Ballinger and Tinkle, 1979; Congdon et al., 1974; Niewiarowski et al., 1997; Vitt et al., 1977), decrease clutch size (Chapple et al., 2002; Dial and Fitzpatrick, 1981; Doughty and Shine, 1998; Smyth, 1974; Wilson and Booth, 1998), reduce offspring size (Chapple et al., 2002) and increase frequency of skipped reproduction (Bernardo and Agosta, 2005). Lizards that have lost their tail, or are in the process of regenerating the tail, are more susceptible to predation as they can no longer use their tails as effectively for predator escape or distraction (Arnold, 1984; Congdon et al., 1974; Dial and Fitzpatrick, 1984; Vitt and Cooper Jr, 1986). To reduce the chance of predation lizards with autotomised tails stay closer to cover (Cooper, 2003; Cooper and Wilson, 2008; Martín and Salvador, 1992; Salvador et al., 1995), decrease their home range size (Salvador et al., 1996) and decrease time foraging (Cooper, 2003; Lu et al., 2010). Increasing time near cover may decrease access to areas for thermoregulation, foraging and finding mates, leading to reduced fitness (Martín and Salvador, 1992, 1993; Salvador et al., 1995). As predation risk has been found to best explain the incidence of tail loss in lizard populations, autotomy is often used as an indicator of predation intensity within populations (Bateman and Fleming, 2009).While there has been limited research on the effects of tail loss on New Zealand skinks, or its use as an indicator of fitness (Barr, 2009), its application in skink species from other countries makes it a viable fitness proxy to investigate.

Parasites are likely to have a detrimental effect on host fitness and increased predation risk can cause further deleterious effects of parasites on the host (Eisen, 2001; Hamilton and Zuk, 1982; Hudson et al., 1998; Møller et al., 1999; Oppliger et al., 1996; Price, 1980; Schall, 1996; Smallridge, 2000). High ectoparasite loads in the viviparous lizard (*Lacerta vivipara*) increased mortality, decreased body mass, lowered endurance, reduced activity, reduced tail regrowth and lowered growth rates (Clobert et al., 2000; Klukowski and Nelson, 2001; Oppliger and Clobert, 1997; Sorci and Clobert, 1995). Similarity, in the bobtail lizard (*Tiliqua rugosa*) increased tick

loads led to smaller home ranges, reduced activity, slower sprint speeds and reduced endurance (Main and Bull, 2000). Parasite infection can lower reproductive success (Atkins, 2004; Dunlap and Schall, 1995; Hare et al., 2010; Oppliger et al., 1996); in the small-scaled skink (*Oligosoma maccanni*) parasite infections reduced pregnancy success from 80% to 6% (Hare et al., 2010). Males infected by the malarial parasite *Plasmodium mexicanum* displayed fewer courtship rituals, had altered sexually coloration, smaller testes (Dunlap and Schall, 1995) and reduced social activity (Schall and Sarni, 1987). Parasites have also been found to negatively influence social status (Dunlap and Schall, 1995), reduce competitive ability (Schall, 1992), and decrease body condition in their hosts (Dunlap and Mathies, 1993; Godfrey et al., 2010; Wozniak et al., 1996). In some cases, parasites can transmit pathogens in their saliva to hosts (Aeschlimann, 1991; Camin, 1948; Dunlap and Mathies, 1993; Smallridge, 2000). Increased predation pressure has been found to increase stress and decrease body condition in lizards (Martín and López, 1999a), which may decrease their ability to allocate resources to parasite defence (Oppliger et al., 1998; Schuster and Schaub, 2001). Thus, the level of parasite infection may be an indicator of the level of predation stress in a population. The chigger mite *Odontacarus lygosomae* commonly infects many species of lizard in New Zealand (Reardon and Norbury, 2004). It was chosen as an indicator of parasite load as it is a large ectoparastite and easy to quantify.

Methods

The northern grass skink (*Oligosoma polychroma*, clade 1b; Liggins et al., 2008) and glossy brown skink (*O. zelandicum*) are endemic to New Zealand. They are both largely diurnal and give birth to live young (Whitaker, 2000). The northern grass skink is widely distributed throughout central and eastern New Zealand (Jewell, 2011). It typically lives in densely-vegetated grassland or shrubland from the littorial to subalpine zones (Freeman, 1997; Whitaker, 2000). It is most active during the middle of the day, about 6-9 hrs after sunrise (Freeman, 1997). The glossy brown skink is found in the Marlborough Sounds, Wellington, the western North Island, and North Westland in the South Island (Whitaker, 2000). They typically live in grasslands, shrublands and open forest (Whitaker, 2000). Glossy brown skinks are listed as at risk on the New Zealand Threat Classification List as they are in partial decline (Hitchmough et al., 2013). They are also on the IUCN Red List, categorised as of least concern (IUCN, 2015).

Both northern grass and glossy brown skinks are considered to be conservation dependant (Hitchmough et al., 2013).

I studied skinks in five populations that varied in the presence or absence of introduced mammalian predators. The names and location of the study sites, the dates each population was studied and the mammalian predators present are listed in Table 4.1. I collected data at four of the sites, and used data from Hoare (2006) for the fifth site. All northern grass skinks collected were over 42 mm snout to vent length (SVL) and thus considered to be adults (Spencer et al., 1998). Glossy brown skinks captured from Maud Island were longer than 58 mm SVL, and thus also considered adult size (East et al., 1995; Neilson et al., 2004). I was unable to catch enough adult glossy brown skinks at Pukerua Bay, thus some juveniles over 42 mm SVL were used in the study in addition to adults. For all sites, other than St. Arnaud, the skinks were released at the end of the research. The St. Arnaud collection was conducted during a long-term population study, so there is a possibility of recaptures occurring. To reduce the probability of resampling the same individuals (and thus pseudoreplication) all skinks were marked with a xylene free permanent silver maker that has been found to last for up to three weeks (Stephens, 2004), though this varies considerably with rainfall and habitat (Lettink, 2007). The recapture rate was found to be low (1.7%), and similar to other studies (Freeman, 1997). Thus, it is unlikely that recaptures significantly influenced this data set.

Each skink captured was identified, sexed by visual inspection of the genitalia, weighed with an electronic balance to 0.01g and the SVL was measured to the nearest 1 mm. Any tail loss and regeneration was recorded and the skink was visually checked for chigger mites by examining the entire body including inside the ears and arm and leg pits. A 10 x magnification hand lens was used to estimate the numbers of mites. Body condition was calculated as defined by Hoare et al., (2006):

$$\frac{Log(mass)}{Log(SVL)}$$

where mass and SVL are measured in grams and millimetres, respectively. All skinks were released at the point of capture.

Statistical analyses

Data were analysed using the program R (R Core Team, 2013). The packages ‘gdata’ (Warnes et al., 2013), ‘lme4’ (Bates et al., 2013) and 'AICcmodavg' (Mazerolle, 2013) were used. To investigate whether sympatry with introduced mammalian predators affected the body condition and proportion of caudal autotomy of skinks I compared ecologically relevant generalised linear models (glm) using Akaike’s Information Criterion for small sample sizes (Burnham and Anderson, 2002). For the body condition models a Gaussian distribution was used with the dependant factor being the body condition index. The fixed factors were: treatment (presence or absence of mammalian predators), species (northern grass or glossy brown skink), number of mites, sex, and the presence or absence of caudal autotomy. A binomial distribution was used for the caudal autotomy models with the dependant factor being the presence or absence of caudal autotomy. The fixed factors were: treatment, species, number of mites, sex, and the skink’s body condition. The null model, all one way models and all additive models were compared, as well as two, three and four way interactive models. Five way interactive models were not compared because the number of terms was too great for the number of observations (444). If a model was too complex for the data and failed to converge, or had too high of an eigenvalue, it was removed from the model compassion.

No mites were found on skinks from Maud Island. Therefore there were insufficient degrees of freedom to perform an Akaike’s Information Criterion for small sample sizes (AICc) to investigate whether sympatry with introduced mammalian predators affected the number of chigger mites on skinks. Instead I explore these patterns using graphical analyses.

Results

The total sample size was 444 individuals, made up of 387 northern grass skinks and 57 glossy brown skinks (Table 4.1). Of the northern grass skinks, 30 were from North Brother Island (20 female, 10 male), 35 from Manaroa (13 female, 22 male) and 322 from the St. Arnaud area (148 female, 174 male; Table 4.1). For glossy brown skinks, 30 were captured on Maud Island, half of each sex, and 27 from Pukerua Bay (20 female, 7 male; Table 4.1). Greater repetition of sites with and without mammalian predators would have been beneficial but was not possible due to logistic constraints.

Body condition

There was a high variation in the body condition index of the skinks, ranging from 0.003 (47 mm SVL, 1.01 g) to 0.562 (79 mm SVL, 11.67 g). For northern grass skinks, the lowest mean body condition was in St. Arnaud (0.23) and highest in Manaroa (0.37; Table 4.2). For glossy brown skinks, body condition was lower in Pukerua Bay (0.31) than on Maud Island (0.34; Table 4.2). There was a strong positive linear relationship between body condition and SVL (Figure 4.1). The relationship is slightly stronger in northern grass skinks (slope = 0.013, $t = 44.470$, df_{386}, $P < 0.001$, $R^2 = 0.828$; Figure 4.1) than glossy brown skinks (slope = 0.009, $t = 9.130$, df_{56}, $P < 0.001$, $R^2 = 0.602$; Figure 4.1). An interactive model containing the factors of species, caudal autotomy and predator presence had the greatest influence on body condition (AICc weight = 0.23; Table 4.3), followed by an interactive model containing the factors species, sex and caudal autotomy (AICc weight = 0.20; Table 4.3), and the additive model of treatment, species, sex and caudal autotomy (AICc weight = 0.17; Table 4.3).

For northern grass skinks from areas with mammalian predators present, those with caudal autotomy had higher body condition than those without caudal autotomy (Figure 4.2 A). In contrast, the opposite pattern is seen in areas without mammalian predators present (Figure 4.2 A). In these areas, skinks with caudal autotomy had lower body condition than those without caudal autotomy (Figure 4.2 A). The relationship between caudal autotomy and the presence of mammalian predators in glossy brown skinks was different to that of northern grass skinks. In areas with mammalian predators present skinks without caudal autotomy had higher body condition than those with caudal autotomy (Figure 4.2 B). In areas without mammalian predators present there was no significant difference in the body condition of glossy brown skinks with and without caudal autotomy (Figure 4.2 B).

Female northern grass skinks with caudal autotomy have higher body condition than those without (Figure 4.3 A). The same pattern is present for male northern grass skinks, but it is not as strong (Figure 4.3 A). In contrast, female glossy brown skinks with caudal autotomy have lower body condition than those with caudal autotomy (Figure 4.3 B). Male glossy brown skinks with caudal autotomy have a slightly higher median body condition that those without, but the variance in body condition are similar (Figure 4.3 B).

When the data for both species is combined, body condition is higher in areas without mammalian predators present (Figure 4.4 A), glossy brown skinks have higher body condition than northern grass skinks (Figure 4.4 B), males have a slightly higher body condition than females (Figure 4.4 C), and skinks with caudal autotomy have higher body condition than those without caudal autotomy (Figure 4.4 D).

Caudal autotomy

The Pukerua Bay brown skink population had the lowest proportion of caudal autotomy of any site (30%), followed by the St. Arnaud northern grass skink population (42%), the Maud Island brown skink population (47%), the Manaroa northern grass skink population (62%) and lastly the North Brother Island northern grass skink population (77%) (Table 4.2). An interactive model containing the factors: species, body condition and treatment had the greatest influence on the prevalence of caudal autotomy (AICc weight = 0.75; Table 4.4). This is effectively the same model that was the best predictor of body condition (Table 4.3, Figure 4.2).

Mites

On North Brother Island 53% of northern grass skinks had chigger mites, while 15% of the skinks from St. Arnaud had them, and no mites were found on skinks from Manaroa (Table 4.2). No chigger mites were found on glossy brown skinks from Maud Island, while 19% of the individuals from Pukerua Bay had some (Table 4.2). The presence of mammalian predators did not significantly affect the mite load for northern grass skinks (Figure 4.5).

Discussion

Body condition

Body condition decreased significantly in areas with mammalian predators present. This was evident in both northern grass and glossy brown skinks. Similar patterns have been seen in lizards both overseas (Amo et al., 2006; Amo et al., 2007a) and in New Zealand (Christmas, 1995). This may be due to the skinks responding to increased predation risk by increasing refuge use (Martín and López, 1999a, b; Sih et al., 1992) and therefore decreasing their time spent foraging and thermoregulating (Amo et al., 2007b; Martín and López, 1999a). It may also be due to increased episodes of fleeing at high speeds, which is also a costly antipredator behaviour (Amo et al., 2007a; Christian et al., 1997; Civantos et al., 2010; Gleeson and Hancock, 2002).

This decline in body condition could have serious conservation implications because body condition is intimately linked to an organism's health (Peig and Green, 2009). A decrease in body condition can reduce the short and long-term fitness of lizards because the amount of stored fat affects survival and reproductive success (Andren and Nilson, 1983; Ballinger, 1977; Civantos and Forsman, 2000; Civantos et al., 1999; Ferguson and Fox, 1984; Laurie and Brown, 1990; Pond, 1981). Therefore, the population declines seen in New Zealand lizards may be due to both direct predation as well as non-lethal predation effects. By increasing food sources, safe thermoregulation areas, and/or predator safe refuges (Sinclair et al., 1998; Souter et al., 2004), it may be possible to reduce the effects of sub-lethal predation by mammal predators and thus increase skink survival and reproduction, though to date this has not proved successful in New Zealand (Lettink et al., 2010).

Glossy brown skinks had higher body condition than northern grass skinks. This may be due to a natural difference in the size to weight ratio in the two species, or the smaller sample size of glossy brown skinks (57) compared to northern grass skinks (387). In addition, there may have been size and condition selection bias in the sampling of glossy brown skinks as they were used in the behavioural experiment (Chapter 5), and thus healthy looking individuals of similar size were collected. This bias is not present in the data collected on northern grass skinks from the St. Arnaud area and North Brother Island, as all adult skinks captured were used in this study. Regardless of this potential selection bias, the findings of this study are still relevant because if anything, this selection bias should have decreased the probability of finding fitness differences between the brown skink populations.

Overall, skinks with caudal autotomy had higher body condition than skinks without. This is surprising as it would be expected that body condition would decrease due to loosing part of the tail, and the potential decreased time foraging and thermoregulating (Cooper, 2003; Cooper and Wilson, 2008; Lu et al., 2010; Martín and Salvador, 1992, 1993; Salvador et al., 1995; Salvador et al., 1996). This pattern is dominated by the northern grass skink data with predators present, as it is the only group to show an increase in body condition with caudal autotomy, and it is based on a larger sample. There are multiple hypotheses to explain this pattern in northern grass skinks. (1) Smaller/lower body condition skinks may be more vulnerable to lethal predation by mammalian predators than larger skinks because they are not as healthy and have fewer energy

reserves to escape predation. Therefore, the lower body-condition skinks observed in this study are those that are more likely to not have had a predator encounter. (2) Skinks with higher body condition outcompete smaller skinks for the best refuges, which may protect them from nocturnal mammal predators. (3) Due to the positive relationship between body condition and SVL, larger individuals may be predated more frequently than smaller individuals by mammalian predators. Therefore the probability of caudal autotomy will increase with the size of the individual as they are more likely to be attacked than smaller individuals. As this pattern was not seen in populations without mammalian predators present, it is not solely due to larger individuals being older and thus more likely to have encountered a predator due to time alone. In New Zealand, larger species of reptiles appear are more vulnerable to predation than smaller species (Whitaker, 1978). This predation bias may also exist within populations. (4) Large skinks may be more likely to need to use caudal autotomy to escape mammalian predators than natural predators. New Zealand lizards co-evolved with a suite of largely visually-oriented avian (Oliver, 1955) and reptilian predators, and thus they evolved anti-predator strategies such as cryptic coloration and secretive behaviour to reduce detection (Worthy and Holdaway, 2002). These behaviours are potentially not effective as anti-predation strategies against mammalian predators that hunt primarily using olfactory cues (Armsworth et al., 2005; King, 2005). Therefore, skinks may be more likely to need to use caudal autotomy to escape a mammalian predator than a native one.

I suggest that hypotheses (1) and (2) are most likely because the frequency of caudal autotomy was lower in areas with mammalian predators than without. This indicates that more predation encounters with mammalian predators end in lethal predation rather than with caudal autotomy. The fact that in female northern grass skinks exhibited higher body condition with caudal autotomy than males, suggests that females may be more vulnerable to predation, as has also been found in Chapter 2. This may be due to females being less agile when pregnant (Bauwens and Thoen, 1981; Shine, 1980; Sinervo et al., 1991). The possibility that skinks with increased body condition are more likely to escape mammalian predators via losing their tail has conservation implications. By increasing body condition through habitat manipulation it may be possible to reduce lethal predation by mammal predators (Sinclair et al., 1998; Souter et al., 2004). Why this pattern was seen in common skinks and not brown skinks may be due to behavioural or habitat differences or the selection bias in the sampling. I recommend further

research to investigate the reasons for this pattern in northern grass skinks and to see whether it exists in other species.

Caudal autotomy

For both northern grass and glossy brown skinks caudal autotomy was more common in areas were mammalian predators were not present. The high prevalence of caudal autotomy in the North Brother Island population of northern grass skinks (77%) may be due to the presence of increased natural predators such as birds and spotted skinks (*O. lineoocellatum*). In addition, tails can be lost in intraspecific aggressive encounters (Congdon et al., 1974; Jennings and Thompson, 1999), and as the population density of the northern grass skink is much higher on North Brother Island (Keall et al., 2001) than in either of the other two sites (J Monks *pers. comm*.), such encounters are more likely. The prevalence of autotomy in the Manaroa population (62%) may be higher than that of the St. Arnaud population (42%) because weka (*Gallirallus australis*), a natural predator, are common in Manaroa, but rare in the St. Arnaud area. The reasons for the higher prevalence of caudal autotomy in glossy brown skinks from mammalian predator-free Maud Island (47%) compared to Pukerua Bay, where mammalian predators are present (30%), may be due to similar reasons. Glossy brown skinks and native birds are much more abundant on Maud Island than Pukerua Bay (*pers. obs*.).

Natural predators such as weka, falcon (*Falco novaeseelandiae*), swamp harrier (*Circus approximans*) and kingfisher (*Todiramphus sanctus*) may have a greater influence on the frequency of caudal autotomy in the skink population than introduced mammalian predators because the native predators are active diurnally. In contrast, the introduced mammalian predators are nocturnal, and are more likely to attack sleeping skinks, which may have little time to escape. Thus, skinks may escape native predators more often via caudal autotomy than introduced predators. A study in California on five species of lizard showed no correlation between predator intensity and tail loss (Jaksić and Greene, 1984). Likewise, tail loss in Duvaucel's gecko was the least frequent on an island from which rats had been eradicated compared to rat-free and rat-inhabited islands, suggesting rat predation pressure does not account for the majority of tail loss (Christmas, 1995).

The frequency of tail loss may instead reflect the inefficiency of predators rather than the intensity of predation, as the better a predator is at catching the skink the less prevalent autotomy

will be in the population (Chapple and Swain, 2004; Jaksić and Greene, 1984; Medel et al., 1988). Thus, caudal autotomy may not be a good measure of predation pressure as it is only applicable if a skink has the same likelihood of escaping each type of predator present at each site (Jaksić and Greene, 1984; Medel et al., 1988; Schall and Pianka, 1980). This fitness proxy suggests that skinks may be more fit on the mainland than predator-free islands. This implies that the skink population decreases observed on the mainland are almost exclusively due to lethal predation, not sub-lethal predation effects, as mammalian predators are much more efficient and prolific predators on skinks than are native avian and reptilian predators (Case and Bolger, 1991; Salo et al., 2007). Indeed, mammals may be so efficient at catching skinks that most encounters are lethal and thus tail autotomy appears less common in sympatry despite higher overall levels of predation. As a consequence, tail autotomy by itself does not appear to be a reliable fitness measure, nor is it likely to be as important in limiting population size as lethal predation.

Chigger mite load

The northern grass skink did not show increased mite load in areas with mammalian predators. In contrast, the percentage of northern grass skinks with chigger mites was highest on North Brother Island (no mammalian predators) and the least in Manaroa (mammalian predators present) where no mites were found. This may be due to the higher population density of skinks on North Brother Island compared with the other sites (J Monks, *pers. comm.*). Lizards are known to acquire mites when they share favourable places such as basking spots or refuges (Amo et al., 2004b), and thus are more likely to be infected in areas with higher population densities. The differences in mite load could also be due to different habitats. For example, rock outcroppings have been found to be more favourable to mite transmission than dense grass and shrublands due to their stable microclimate (Reardon and Norbury, 2004).

No chigger mites were found on glossy brown skinks from mammalian predator-free Maud Island, while some were found on individuals from Pukerua Bay where mammalian predators are present. This pattern could be due to stress caused by increased predation pressure in Pukerua Bay reducing the ability of the immune system of a skink to fight mite infection (Oppliger et al., 1998; Schuster and Schaub, 2001). It may also be due to other factors such as habitat differences between the sites (Reardon and Norbury, 2004), or it could simply be the result of mites being absent as they have never been found on the island (Danielle Middleton, *pers. comm*., 2015).

Further research at a larger scale addressing these factors would need to be conducted to confirm whether there is a difference, and if so, what is causing it.

Conclusion

This study shows evidence that introduced mammalian predators are causing sub-lethal predation effects on northern grass and glossy brown skinks. Body condition was significantly lower in areas with mammalian predators present. This has serious conservation repercussions because it shows that lizard populations may not only be in decline from direct predation, but also additional stresses associated with that predation that may lead to reduced reproductive output. The complex interactions between body condition, caudal autotomy, sex and species highlights that different species, sexes and size classes/body conditions within species, may be experiencing different levels of predation pressure. The possibility that skinks with increased body condition are more likely to escape mammalian predators via losing their tail has conservation implications. It may be possible to reduce lethal predation and/or sub-lethal predation effects by mammal predators by increasing body condition through habitat manipulation (Sinclair et al., 1998; Souter et al., 2004).

Regardless of its influence on body condition, caudal autotomy does not appear to be a good fitness indicator because it is only applicable if a skink has the same likelihood of escaping each type of predator present at each site (Jaksić and Greene, 1984; Medel et al., 1988; Schall and Pianka, 1980). As mammalian predators are much more efficient and prolific predators on skinks than native avian and reptilian predators (Case and Bolger, 1991; Salo et al., 2007), it is probably not a reliable proxy for fitness in this case. The finding that caudal autonomy was more common in areas without mammalian predators implies that most predation encounters with mammalian predators end in lethal predation. Like caudal autotomy, mite load was not a good indication of fitness. Chigger mites may not have been present at all of the sites, and the probability of mite transmission is influenced by skink density (Amo et al., 2004b) as well as the skinks health (Oppliger et al., 1998; Schuster and Schaub, 2001). Therefore I do not suggest it as a fitness indicator for New Zealand skinks.

This research suggests that introduced mammalian predators may be causing significant sub-lethal effects on native lizards. It builds on previous work that showed a similar pattern in Duvaucel's geckos (Christmas, 1995). I highly recommend further investigation into how wide spread this is among species and populations. I also suggest direct analysis into the degree decreased body condition affects the long and short-term fitness of New Zealand lizards.

Figures and Tables

Table 4.1: List of collection sites. For each site, the location, dates of collection, species of skink present, method of capture, and types of mammalian predators present are given.

Location of site	Date	Species	Skinks caught	Collection method	Mammalian predators
North Brother Island, Marlborough Sounds (S 41 º10548, E 174 º44434)	24- 27 February 2004 (Hoare, 2006b)	Northern grass skink	30	Pit-fall traps	None
Manaroa, Marlborough Sounds (S 41 º 12966785, E 174 º 04111862)	17 February - 23 March 2011	Northern grass skink	35	Pit-fall traps Corrugated iron	Hedgehogs, mice, rats, possums, stoats, weasels, cats
St. Arnaud , Nelson/Marlborough region (41.8033° S, 172.8450° E)	November - March 2010/2011 and 2011/2012	Northern grass skink	322	Pit-fall traps	Hedgehogs, mice, rats, possums, stoats, weasels, cats, dogs
Maud Island, Marlborough Sounds, (S 41 º 03436983, E 173 º 91142848)	24 March 2011	Glossy brown skink	30	Shearwater nest boxes	None
Pukerua Bay, Wellington (S 41 º 03003187, E 174 º 88397598)	13 and 16 January 2012	Glossy brown skink	27	Pit-fall traps	Hedgehogs, mice, ship rats, stoats, weasels and cats

Table 4.2: The body condition index and percentage of individuals with mites and caudal autotomy for each: site, presence or absence of mammalian predators and species.

Site	**Mammalian predators**	**Skink species**	**Mites (%)**	**♀ with mites (%)**	**♂ with mites (%)**	**Body condition** log(mass)/ log(SVL)	**Caudal autotomy (%)**
North Brother Island	No	Northern grass	53	50	60	0.30	77
Manaroa	Yes	Northern grass	0	0	0	0.37	62
St. Arnaud	Yes	Northern grass	15	16	12	0.23	42
Maud Island	No	Glossy brown	0	0	0	0.34	47
Pukerua Bay	Yes	Glossy brown	19	15	29	0.31	30

Table 4.3: AICc comparison of models used to evaluate variables as predictors of the body condition of a skink. Treatment = presence or absence of mammalian predators, Species = northern grass or glossy brown skink, CA = presence of caudal autotomy, Mites = number of chigger mites.

Model	K	AICc	ΔAICc	AICc weight	Cumulative Mass	Log Likelihood
Treatment * Species * CA	11	-820.16	0.00	0.23	0.23	421.38
Species * Sex * CA	11	-819.80	0.36	0.20	0.43	421.20
Treatment + Species + Sex + CA	8	-819.50	0.66	0.17	0.60	417.92
Species * CA	7	-818.86	1.29	0.12	0.72	416.56
Treatment + Species + Sex + CA + Mites	9	-818.21	1.95	0.09	0.81	418.31
Treatment + Species + CA	7	-817.49	2.67	0.06	0.87	415.87
Species + Sex + CA	7	-816.22	3.94	0.03	0.90	415.24
Treatment + Species + CA + Mites	8	-816.09	4.07	0.03	0.94	416.21
Treatment * Species * Sex * CA	19	-815.21	4.95	0.02	0.95	427.50
Species + Sex + CA + Mites	8	-814.83	5.32	0.02	0.97	415.58
Species + CA	6	-814.58	5.58	0.01	0.99	413.38
Species + CA + Mites	7	-813.10	7.06	0.01	0.99	413.68
Species * CA * Mites	11	-812.08	8.08	0.00	1.00	417.34
Treatment * Species * CA * Mites	17	-808.82	11.34	0.00	1.00	422.13
Treatment * CA	7	-808.71	11.45	0.00	1.00	411.48
Treatment + Species + Sex	5	-807.79	12.37	0.00	1.00	408.96
Species * Sex * CA * Mites	18	-807.55	12.61	0.00	1.00	422.58
Treatment + Species + Sex + Mites	6	-806.25	13.91	0.00	1.00	409.22
Treatment * Sex * CA	11	-805.58	14.58	0.00	1.00	414.10
Treatment + Species	4	-805.40	14.76	0.00	1.00	406.74
Treatment + Sex + CA	7	-804.09	16.07	0.00	1.00	409.17
Treatment + Species + Mites	5	-803.76	16.40	0.00	1.00	406.95
Treatment * Species * Sex	9	-803.56	16.60	0.00	1.00	410.99
Treatment * Species	5	-803.54	16.62	0.00	1.00	406.84
Treatment + CA	6	-803.26	16.90	0.00	1.00	407.73
Treatment + Sex + CA + Mites	8	-802.45	17.70	0.00	1.00	409.39
Treatment * CA * Mites	11	-801.68	18.47	0.00	1.00	412.15
Treatment + CA + Mites	7	-801.57	18.59	0.00	1.00	407.91
Species + Sex	4	-801.11	19.05	0.00	1.00	404.60
Species * Sex	5	-800.17	19.99	0.00	1.00	405.15
Species + Sex + Mites	5	-799.45	20.71	0.00	1.00	404.79
Species	3	-799.23	20.92	0.00	1.00	402.64
Species	3	-799.23	20.92	0.00	1.00	402.64
Treatment * Species * Mites	8	-797.91	22.25	0.00	1.00	407.12
Species + Mites	4	-797.50	22.66	0.00	1.00	402.80
Treatment + Sex	4	-796.54	23.62	0.00	1.00	402.31
Species * Mites	5	-795.99	24.16	0.00	1.00	403.07
Treatment * Sex	5	-795.34	24.82	0.00	1.00	402.74
Treatment	3	-795.25	24.91	0.00	1.00	400.65
Treatment	3	-795.25	24.91	0.00	1.00	400.65
Treatment + Sex + Mites	5	-794.77	25.38	0.00	1.00	402.46
Species * Sex * Mites	9	-793.80	26.36	0.00	1.00	406.11
Treatment + Mites	4	-793.44	26.72	0.00	1.00	400.77
Treatment * Species * Sex * Mites	15	-792.60	27.56	0.00	1.00	411.86
Treatment * Mites	5	-792.46	27.70	0.00	1.00	401.30
Treatment * Sex * CA * Mites	19	-791.42	28.74	0.00	1.00	415.60

Treatment * Sex * Mites	9	-789.66	30.50	0.00	1.00	404.04
Ca	5	-785.74	34.42	0.00	1.00	397.94
Ca	5	-785.74	34.42	0.00	1.00	397.94
Sex + CA	6	-785.44	34.72	0.00	1.00	398.81
Sex * CA	7	-784.34	35.82	0.00	1.00	399.30
CA + Mites	6	-783.83	36.33	0.00	1.00	398.01
Sex + CA + Mites	7	-783.54	36.62	0.00	1.00	398.90
CA * Mites	7	-781.77	38.39	0.00	1.00	398.01
Sex * CA * Mites	11	-777.71	42.45	0.00	1.00	400.16
Null	2	-774.33	45.83	0.00	1.00	389.18
Sex	3	-774.28	45.87	0.00	1.00	390.17
Sex	3	-774.28	45.87	0.00	1.00	390.17
Mites	3	-772.35	47.81	0.00	1.00	389.20
Mites	3	-772.35	47.81	0.00	1.00	389.20
Sex + Mites	4	-772.31	47.85	0.00	1.00	390.20
Sex * Mites	5	-771.75	48.41	0.00	1.00	390.94

Table 4.4: AICc comparison of models used to evaluate variables as predictors of the probability of skink having caudal autotomy. Treatment = presence or absence of mammalian predators, Species = northern grass or glossy brown skink, BC = body condition, Mites = number of chigger mites.

Model	K	AICc	ΔAICc	AICc weight	Cumulative Mass	Log Likelihood
Treatment * Species * BC	8	584.42	0.00	0.75	0.75	-284.04
Treatment * BC	4	589.11	4.69	0.07	0.82	-290.51
Treatment + Species + BC	4	589.47	5.06	0.06	0.88	-290.69
Treatment + Species + BC + Mites	5	590.74	6.33	0.03	0.91	-290.30
Treatment + Species + Sex + BC	5	591.50	7.08	0.02	0.93	-290.68
Treatment * Species * BC * Mites	14	591.85	7.43	0.02	0.95	-281.44
Treatment + Species + Sex + BC + Mites	6	592.77	8.36	0.01	0.96	-290.29
Treatment * Species * Sex * BC	16	593.04	8.63	0.01	0.97	-279.89
Species * BC	4	593.63	9.21	0.01	0.98	-292.77
Treatment * BC * Mites	8	593.72	9.30	0.01	0.99	-288.69
Treatment * Sex * BC	8	595.09	10.67	0.00	0.99	-289.38
Species + BC	3	596.90	12.48	0.00	0.99	-295.42
Species * Sex * BC	8	597.11	12.69	0.00	0.99	-290.39
Species * BC * Mites	8	597.59	13.17	0.00	1.00	-290.63
Species + BC + Mites	4	597.98	13.56	0.00	1.00	-294.94
Treatment + BC	3	598.20	13.78	0.00	1.00	-296.07
Species + Sex + BC	4	598.85	14.44	0.00	1.00	-295.38
Bc	2	599.63	15.21	0.00	1.00	-297.80
Bc	2	599.63	15.21	0.00	1.00	-297.80
Treatment + BC + Mites	4	599.73	15.31	0.00	1.00	-295.82
Species + Sex + BC + Mites	5	599.93	15.51	0.00	1.00	-294.89
Treatment + Sex + BC	4	600.21	15.79	0.00	1.00	-296.06
BC + Mites	3	600.99	16.57	0.00	1.00	-297.47
Sex + BC	3	601.66	17.24	0.00	1.00	-297.80
Treatment + Sex + BC + Mites	5	601.75	17.34	0.00	1.00	-295.81
BC * Mites	4	602.89	18.48	0.00	1.00	-297.40
Sex + BC + Mites	4	603.02	18.61	0.00	1.00	-297.47
Sex * BC	4	603.07	18.66	0.00	1.00	-297.49
Treatment + Species	3	603.60	19.19	0.00	1.00	-298.77
Treatment * Species	4	604.67	20.26	0.00	1.00	-298.29
Treatment + Species + Mites	4	605.07	20.66	0.00	1.00	-298.49
Treatment + Species + Sex	4	605.56	21.14	0.00	1.00	-298.73
Treatment + Species + Sex + Mites	5	607.05	22.64	0.00	1.00	-298.46
Treatment	2	608.63	24.21	0.00	1.00	-302.30
Treatment	2	608.63	24.21	0.00	1.00	-302.30
Treatment * Species * Mites	7	608.86	24.44	0.00	1.00	-297.30
Treatment * Mites	4	609.89	25.47	0.00	1.00	-300.90
Treatment + Mites	3	610.25	25.84	0.00	1.00	-302.10
Sex * BC * Mites	8	610.40	25.99	0.00	1.00	-297.04
Treatment + Sex	3	610.45	26.03	0.00	1.00	-302.20
Treatment + Sex + Mites	4	612.10	27.68	0.00	1.00	-302.01
Treatment * Sex	4	612.31	27.89	0.00	1.00	-302.11
Treatment * Species * Sex	8	612.66	28.25	0.00	1.00	-298.17
Null	1	613.92	29.50	0.00	1.00	-305.95
Species	2	614.67	30.25	0.00	1.00	-305.32
Species	2	614.67	30.25	0.00	1.00	-305.32

Mites	2	615.33	30.91	0.00	1.00	-305.65
Mites	2	615.33	30.91	0.00	1.00	-305.65
Sex	2	615.87	31.46	0.00	1.00	-305.92
Sex	2	615.87	31.46	0.00	1.00	-305.92
Species * Mites	4	615.90	31.48	0.00	1.00	-303.91
Species + Mites	3	615.97	31.55	0.00	1.00	-304.96
Species + Sex	3	616.68	32.26	0.00	1.00	-305.31
Treatment * Sex * Mites	8	616.91	32.50	0.00	1.00	-300.29
Sex + Mites	3	617.31	32.89	0.00	1.00	-305.63
Species + Sex + Mites	4	617.99	33.58	0.00	1.00	-304.95
Species * Sex	4	618.65	34.23	0.00	1.00	-305.28
Sex * Mites	4	619.34	34.92	0.00	1.00	-305.63

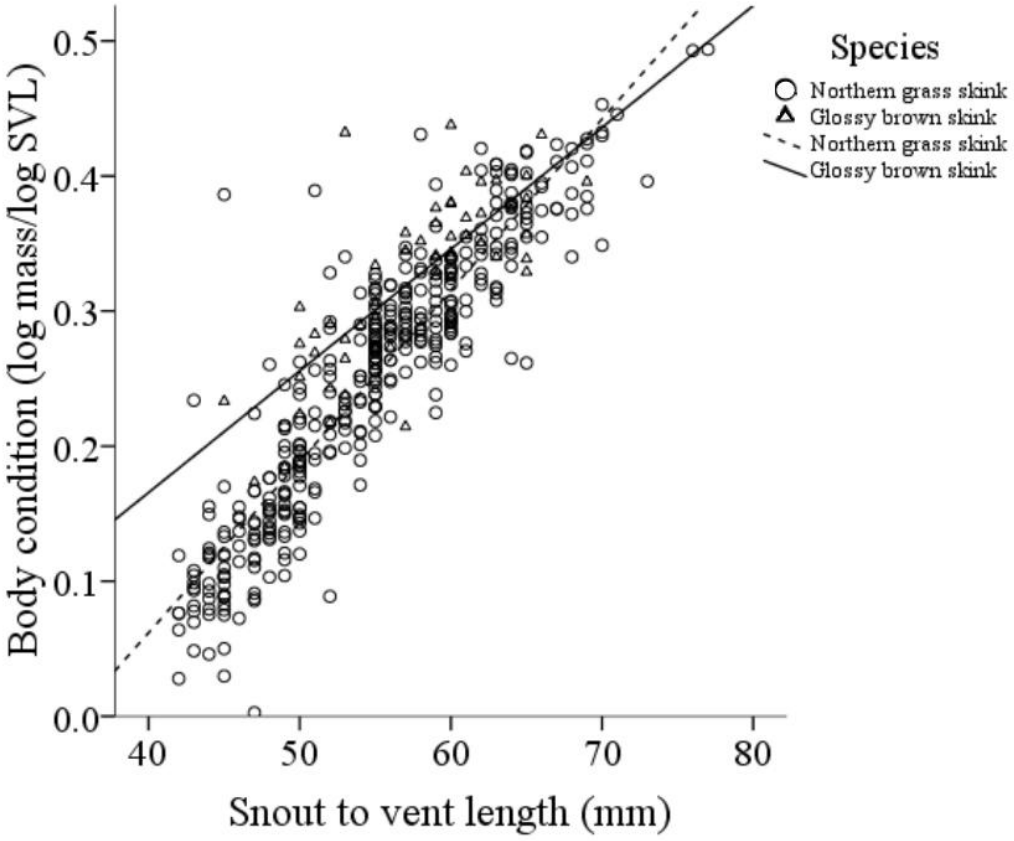

Figure 4.1: A comparison of the relationship between body condition and snout to vent length for northern grass and glossy brown skinks. Linear trend lines shown. Northern grass skink R^2 = 0.828, glossy brown skink R^2 = 0.602.

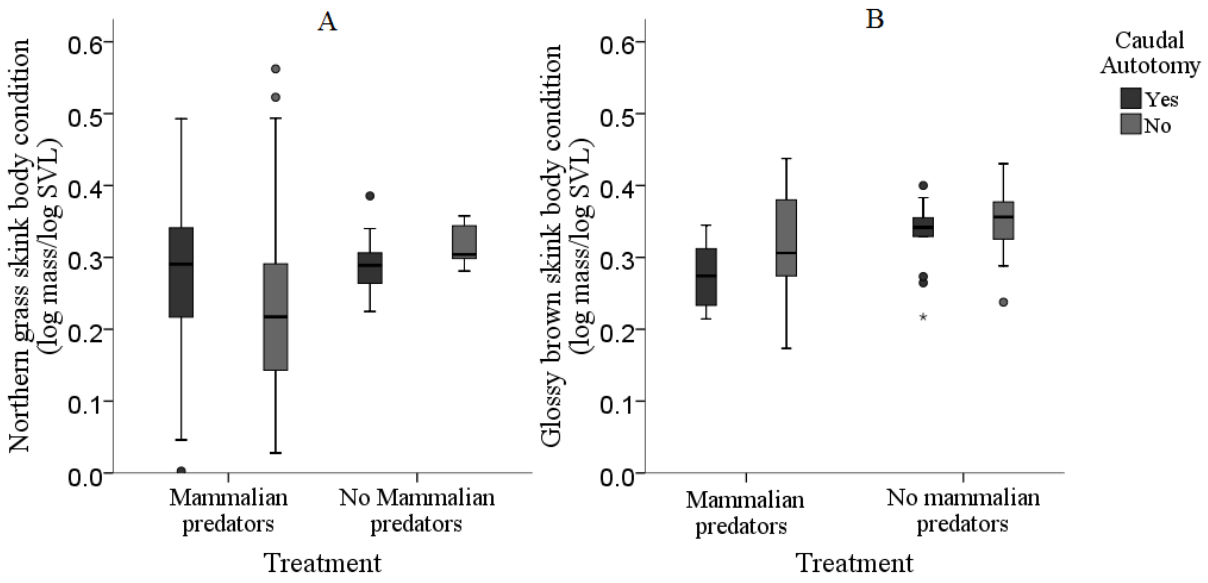

Figure 4.2: A comparison of the relationship between body condition, caudal autotomy and the presence or absence of mammalian predators of (A) northern grass skinks and (B) glossy brown skinks. The dark horizontal line is the median. The upper edge of each box is the upper quartile and the lower edge of each box is the lower quartile. The whiskers include 95% of the data. Open circles represent outliers, and * represent extreme outliers.

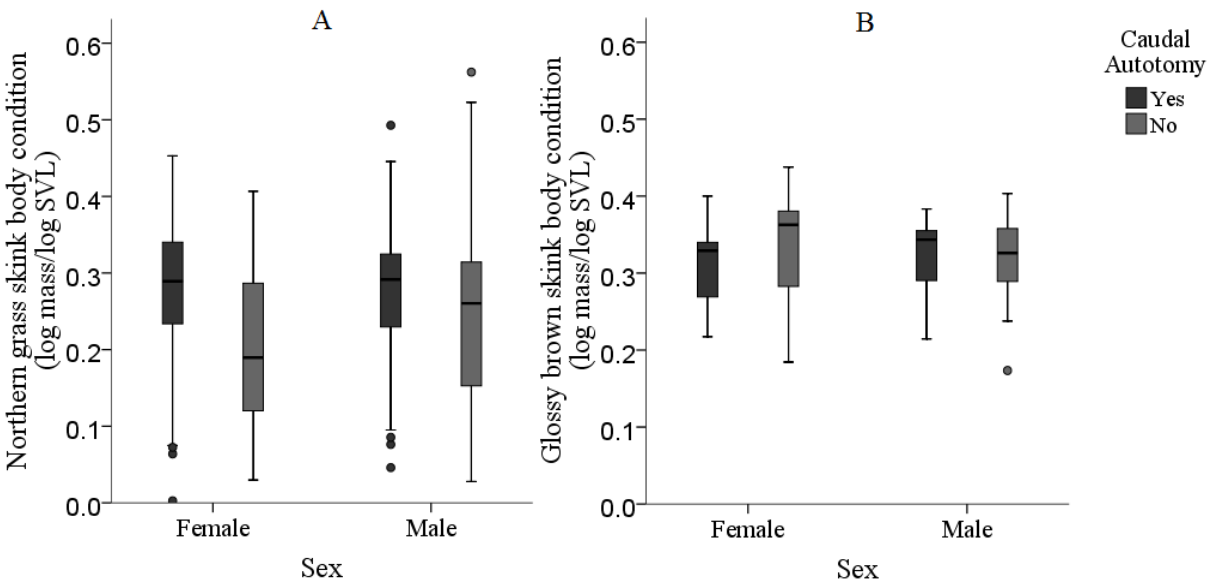

Figure 4.3: A comparison of the relationship between body condition, caudal autotomy and the sex of (A) northern grass skinks and (B) glossy brown skinks. The dark horizontal line is the median. The upper edge of each box is the upper quartile and the lower edge of each box is the lower quartile. The whiskers include 95% of the data. Open circles represent outliers.

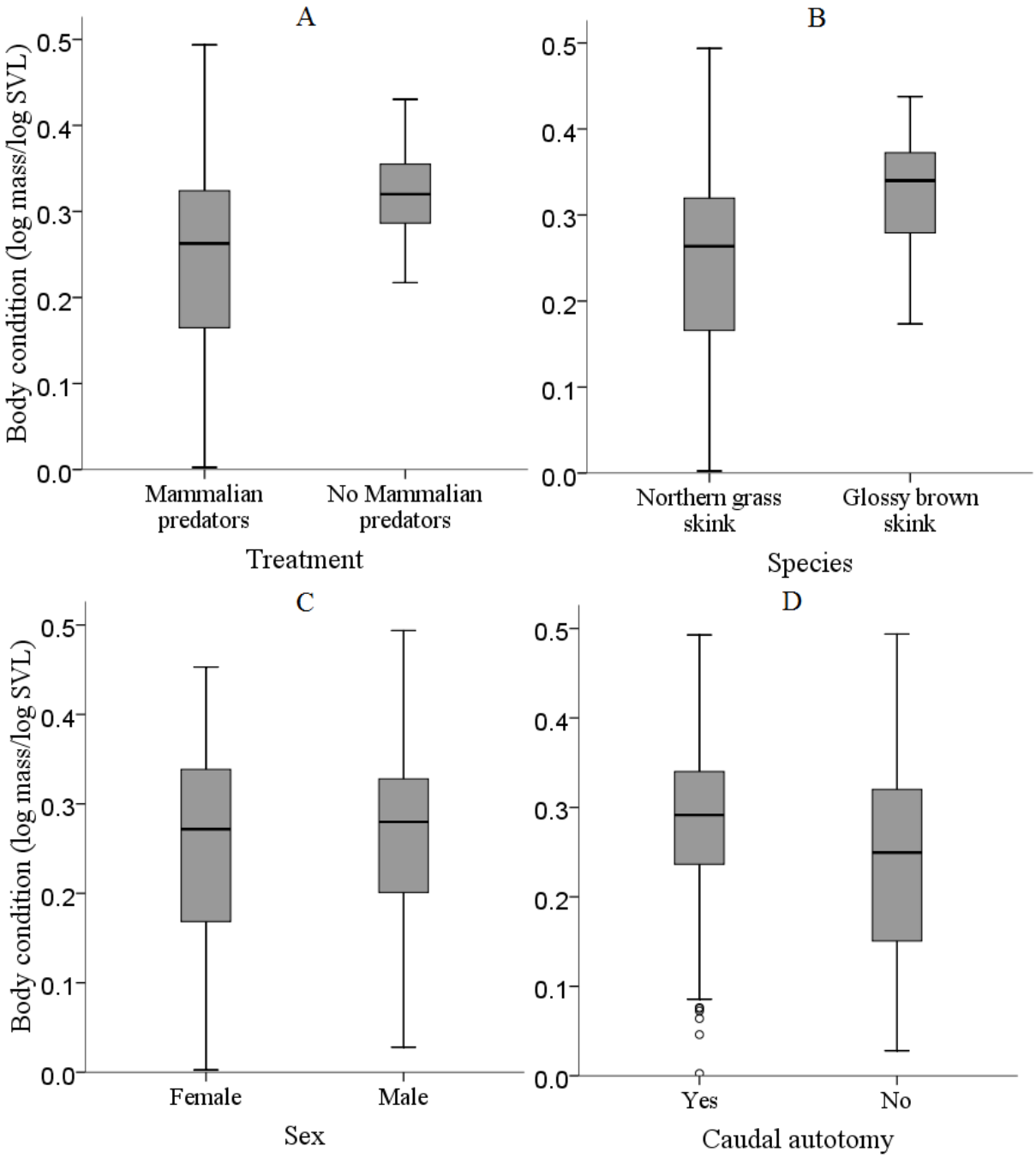

Figure 4.4: A comparison of the relationship between body condition and: (A) treatment, (B) species, (C) sex, and (D) caudal autotomy. The dark horizontal line is the median. The upper edge of each box is the upper quartile and the lower edge of each box is the lower quartile. The whiskers include 95% of the data. Open circles represent outliers.

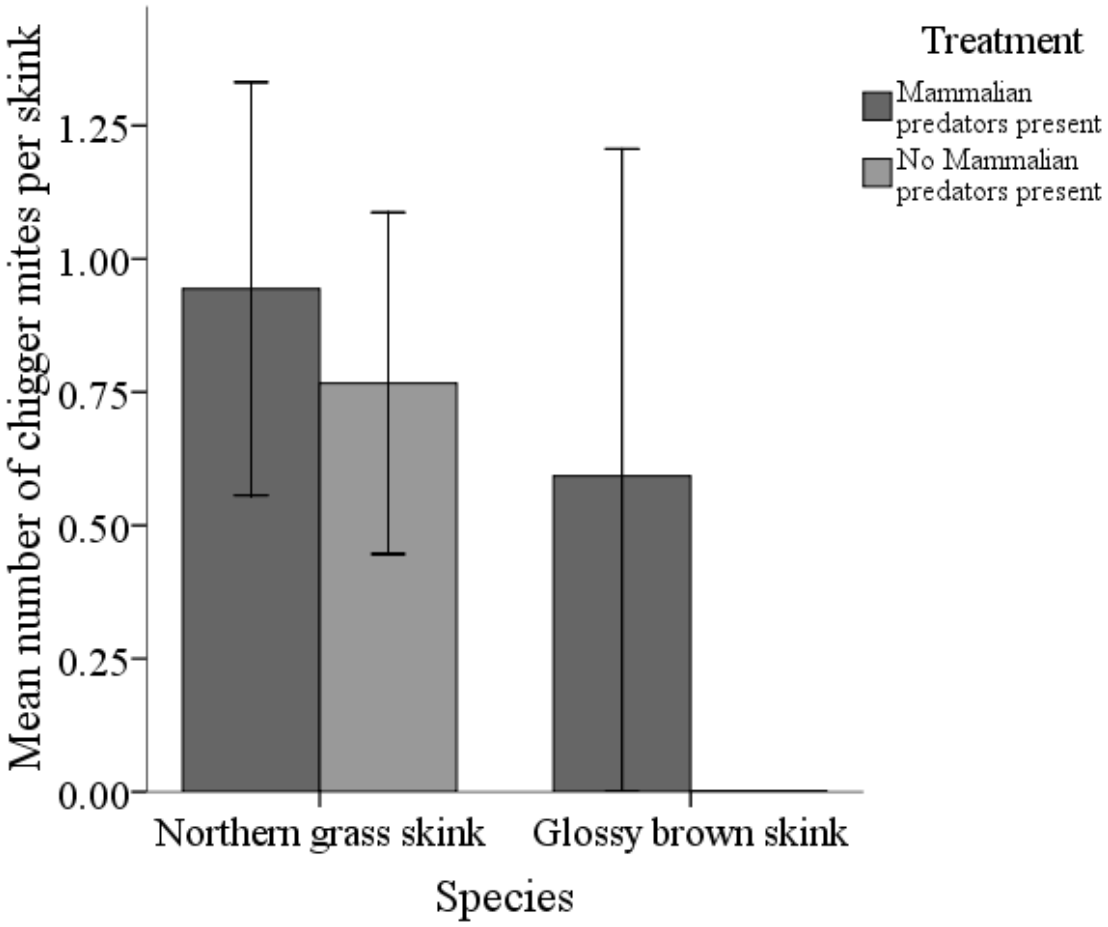

Figure 4.5: The mean number of chigger mites per skink for each species in relation to exposure to introduced mammalian predators. No chigger mites were found on glossy brown skinks from mammalian predator free Maud Island. Error bars show a 95% confidence interval.

Chapter 5: What's that smell? Do New Zealand northern grass and glossy brown skinks avoid the scent of introduced rats or hedgehogs?

Abstract

Avoiding predation requires that a potential prey animal can detect the stimuli associated with a predator and differentiate these from those associated with beneficial or harmless situations. When novel predators are introduced into an ecosystem, the indigenous fauna may lack suitable recognition and anti-predator behaviours, making them vulnerable to predation. I investigated whether two species of indigenous New Zealand skinks, the glossy brown skink (*O. zelandicum*) and the northern grass skink (*Oligosoma polychroma*), have the ability to detect and avoid the faecal scent of two introduced mammalian predators (ship rat [*Rattus rattus*] and hedgehog [*Erinaceus europaeus*]). Each skink was placed in a terrarium with a choice of two retreats, one with either a predator or control scent, and the other one scent-free. The strength of the predator scent was also manipulated. Skinks were filmed for 12 hours to record which retreats were entered and the duration of each visit. Both northern grass skinks and glossy brown skinks showed little avoidance behaviour in response to the experimental presentation of the scent of rats or hedgehogs. However, the skinks spent slightly more time hiding in retreats when hedgehog scent was present than when rat or the positive control scent was present, and glossy brown skinks from Pukerua Bay (mammalian predators present) reduced the number of entries into retreats with increased scent stimulus. In addition, female skinks spent more time hiding in retreats than males, there were significant and differences in behaviours between the two species, and skinks with caudal autotomy spent less time in retreats than those without. These variable responses suggest that either native skinks have not had enough time to evolve extensive avoidance behaviours or that there is not enough selection pressure for these traits to evolve. These findings indicate that indigenous New Zealand skinks have limited avoidance behaviours to the odours of introduced mammalian predators.

Introduction

Predators produce a variety of immediate (visual, tactile, auditory) and non-immediate (odour) cues that can be potentially used by prey to avoid capture (Downes, 2002; Kavaliers and Choleris, 2001). Avoiding predation implies that prey can detect these stimuli and differentiate them from stimuli associated with beneficial or harmless situations (Carlile et al., 2006). The ability to detect predators appears to be innate in most reptiles, though maternal learning and postnatal experience may build on these genetic responses (Greene, 1988). The expression of antipredator mechanisms can also vary geographically if different populations experience differing predation pressures (Greene, 1988).

How reptiles detect potential predators appears related to their feeding system (Greene, 1988), and their evolutionary history (Vitt and Pianka, 2005). Scleroglossan reptiles have an active foraging mode and rely primarily on chemical cues to detect predators (Vitt and Pianka, 2005). This contrasts markedly with the behavioural, physiological and morphological patterns of foraging in iguanid reptiles, which retain an ambush strategy and rely more on vision (Vitt and Pianka, 2005). The chemosensory system of scleroglossans is complex, including olfactory, gustation and vomerolfaction systems (Parsons, 1959; Schwenk, 1995). Active foraging scleroglossans, such as skinks (family Scincidae) have a particularly sophisticated chemosensory system (Cooper Jr, 2000). In addition, for organisms such as skinks that inhabit physically complex habitats, chemosensory cues may be vital in detecting predators as visual cues may be hindered (Kats and Dill, 1998). Chemosensory recognition can be used to detect the presence of a predator as well as additional information on the predator such as its activity level and diet (Kats and Dill, 1998).

The ability to detect a predator and respond appropriately can significantly reduce a individual's probability of being caught (Downes, 2002). A number of studies have demonstrated that reptiles can detect the chemical cues left by predators and this is manifested through increased tongue flicks and/or changes in their behaviour. For example, volmerolfaction is essential for North American pit vipers (Crotalinae) to detect the predatory kingsnake (*Lampropeltis getula*) (Miller and Gutzke, 1999). Similarly, the scent of tuatara (*Sphenodon punctatus*), an ambush predator,

elicits antipredator behaviour in its prey, the green gecko (*Naultinas manukanus*), which is a sit-and-wait predator (Hare et al., 2007; Hoare et al., 2007b).

Long isolation from predator guilds has been shown to lead to the loss of antipredator traits and behaviours in prey species through relaxed selection and genetic drift (Blumstein and Daniel, 2005; Blumstein et al., 2002; Coss, 1999; Magurran, 1999). As a consequence, human-mediated introductions of predators have resulted in range contractions and extinctions of species that previously were geographically isolated from these predators (Cassels, 1984; Worthy and Holdaway, 2002). In a survey of the effects of introduced predators on the abundance and distribution of reptiles, Case and Bolger (1991) found that extinctions and severe reductions in the abundance of native reptiles coincided with the introduction of exotic predators, and that the 'predator-naive' species were affected the most.

New Zealand provides an excellent example of the effect of exotic predators on native reptile populations. Prior to human contact 1250-1300 years ago (Anderson, 1991; Wilmshurst and Higham, 2004), they were no terrestrial mammals present for the last few million years (Worthy et al., 2006), except for three species of bat (Anderson, 1996; Holdaway, 1996; Worthy and Holdaway, 2002). Since then 11 mammalian predators have been introduced; this is more than any other archipelago (Towns et al., 1997). In conjunction with habitat destruction (Towns and Daugherty, 1994), introduced mammalian predators are considered to be the major causes of the extinctions and range restrictions in many native species (Worthy and Holdaway, 2002). Since the arrival of humans (Anderson, 1991; Wilmshurst and Higham, 2004), New Zealand has lost three species of lizard (Bauer and Russell, 1986; Hardy, 1977; Worthy, 1987a) and many of the extant species have drastically reduced populations (Daugherty et al., 1994; Hitchmough et al., 2010). In contrast, reptiles that coevolved with mammalian predators have been found to be less susceptible to introduced mammalian predators (Gibbon et al., 2000).

Hoare (2006) proposed two hypotheses to explain why the New Zealand herptetofauna is susceptible to mammalian predation. Firstly, is it possible that introduced mammals have created additional predation pressure to that of native predators (birds and larger reptiles such as tuatara). This may cause population declines as most native species are characterised by K-selected life

history patterns (Cree, 1994; Newman and Watson, 1985), and are thus easily endangered by increased mortality. This hypothesis is supported by the findings that the larger, longer-lived species are disproportionately affected by introduced mammalian predators (Daugherty et al., 1993; Towns and Daugherty, 1994). The second hypothesis proposes that predation by introduced mammals is different from, rather than simply additional to that of native predators (Blumstein, 2002; Worthy and Holdaway, 2002). It is suggested that the absence of selective pressure by mammalian predators may have caused native species to be less likely to detect and respond appropriately to mammalian predators and/or make them easier for mammals to find and capture (Hoare, 2006b). Native predatory species are primarily visual predators (Meyer-Rochow, 1988; Meyer-Rochow and Teh, 1991; Worthy and Holdaway, 2002). This is reflected in the secretive behaviours and visual crypsis exhibited by native lizards (Hoare, 2006b; Worthy and Holdaway, 2002). These strategies may give New Zealand's reptiles little protection from introduced mammalian predators that hunt primarily via olfactory cues (Armsworth et al., 2005; King, 2005).

It has been found that the endemic Marlborough green gecko can detect the faeces of tuatara, a native predator, from olfactory cues alone (Hoare et al., 2007b). This suggests that olfactory cues are used by native reptiles and that they could use this ability to similarly detect introduced species. Although there has been some research on the chemosensory detection of snake and lizard predators by reptiles (Kats and Dill, 1998), there has been little work on the detection of mammalian predators by reptiles (Cowles, 1938; Hoare, 2006b; Kats and Dill, 1998). Hoare (2006) investigated the behaviour of indigenous skinks and geckos in response to the scent of rats and tuatara. She found little evidence that skinks were able to detect rats but only tested individuals over a short time span. In this study, I investigated the behaviour of the indigenous northern grass skink (*O. polychroma*) and glossy brown skink (*O. zelandicum*) when exposed to the faecal samples of introduced rats (*Rattus rattus*) and hedgehogs (*Erinaceus europaeus*). These two mammals are likely to have preyed upon skinks since their introduction (Jones et al., 2005; Worthy and Holdaway, 2002) and thus it is possible that the skinks have developed the ability to detect and adapt to these novel predators.

Due to the strong ecological effects of some exotic predators, evolutionary changes can occur in their prey, even to the stage of allowing the native species to co-exist with the new predator

(Strauss et al., 2006). Whether or not a native population is capable of responding to evolutionary selection pressure from invaders depends on the demographic impact of the invader, the genetic variability and architecture of the natives, and the evolutionary history of the native population (Strauss et al., 2006). Co-evolution of indigenous species to introduced predators has been found in many species (Bell, 2002; Kiesecker and Blaustein, 1997; Kovacs et al., 2012; Mella et al., 2014; Parsons and Blumstein, 2010; Strauss et al., 2006). For these evolutionary responses to occur the exotics must affect the fitness of native species, these fitness effects must be non-random such that some genotypes increase fitness more than others, and the traits involved must be heritable (Strauss et al., 2006). In New Zealand, evolutionary responses in natives to introduced predators have been observed in the bellbird (*Anthornis melanura*) (Massaro et al., 2008), tree wētā (*Hemideina crassidens*) (Rufaut and Gibbs, 2003), terrestrial arthropods (Bremner et al., 1989), and Duvaucel's geckos (*Hoplodactylus duvaucelii*) as well as other lizards (Hoare et al., 2007c), suggesting it could occur in other native species as well. This study investigated whether anti-predator strategies to novel predators are present in two species of New Zealand's indigenous skinks.

Methods

Northern grass skinks (*Oligosoma polychroma*) and glossy brown skinks (*O. zelandicum*) are endemic to New Zealand. They are both largely diurnal and give birth to live young (Whitaker, 2000). The northern grass skink is widely distributed throughout central and eastern New Zealand (Jewell, 2011). It typically lives in densely-vegetated grassland or shrubland from the littorial to subalpine zones (Freeman, 1997; Whitaker, 2000). It is most active in the middle of the day, about 6-9 hours after sunrise (Freeman, 1997). The northern grass skink clade used in this study is 1b (Liggins et al., 2008).The glossy brown skink is found in the Marlborough Sounds, western North Island from Taranaki to North Westland, as well as Wellington (Whitaker, 2000). They typically live in grasslands, shrublands and open forest (Whitaker, 2000). The northern grass skink clade 1b is not considered threatened (Hitchmough et al., 2013) while the glossy brown skink is considered at risk due to declining populations (Hitchmough et al., 2013). The total area of occupancy for the glossy brown skink is over 100 km^2 but the population is expected to decline 10 -70% (Hitchmough et al., 2013). They are also listed on the

IUCN Red List, categorised as of least concern (IUCN, 2015). Both species are considered conservation dependant (Hitchmough et al., 2013).

The ability of northern grass skinks to avoid the scent of two species of introduced mammalian predators was tested using 28 adult skinks (> 42 mm; as defined by Spencer et al., 1998) that were collected from Manaroa, Marlborough Sounds, New Zealand, between 17 February and 23 March 2011. The sample included 16 males and 12 females. The skinks were caught either in pit-fall traps or collected from under pieces of corrugated tin roofing laid on the ground. A wide range of mammalian predators are likely to be found at Manaroa including hedgehogs, mice (*Mus musculus*), rats, possums (*Trichosurus vulpecula*), stoats (*Mustela erminea*), weasels (*Mustela nivalis*) and feral cats (*Felis catus*).

The ability of glossy brown skinks to avoid the scent of introduced mammalian predators was tested using 24 adults (> 58 mm; as defined by East et. al.,1995 and Neilson et. al., 2004) collected from Maud Island, Marlborough Sounds on 24 March 2011. The sample included 12 male and 12 female adults. They were captured from shearwater nest boxes, which they use as roosts. Maud Island does not, and never has, harboured any introduced mammalian predators. Another 27 adult glossy brown skinks (>42 mm, 5 male and 22 female) were collected from Pukerua Bay, Wellington between 13 and 16 January 2012. In contrast to Maud Island, a wide range of mammalian predators are found at Pukerua Bay including hedgehogs, mice, ship rats, stoats, weasels and cats (Hoare et al., 2007a). Thus, the collection of the same species of skink from both a predator-free island and a mainland site with predators present allowed me to investigate if any potential antipredator defences have developed in the mainland population with introduced predators. Greater replication of sites, treatments and species would have been preferable but was not possible due to practical constraints**.**

Once captured, each skink was placed in an individual black plastic tub (58 cm x 43 cm x 28 cm) lined with fine wood chips. Two retreats were provided, consisting of plastic potting containers (10 cm deep, 8 cm diameter), turned upside down and with a thumb-sized hole in the bottom for an entrance. *Ad libitum* food (mealworms and tinned pear) and water was provided (Figure 5.1). Each skink was sexed, weighed, measured and the presence or absence of caudal autotomy (tail

loss) was recorded. Each skink was allowed to acclimatise to the terrarium for at least three days before the experiment was started.

To assess the ability of skinks to detect different odours, including that of predatory mammals, each skink was presented with three different scent treatments: rat, hedgehog and a positive control scent (perfume). Faecal samples of rats and hedgehogs were used as potential cues that a skink might use to detect the nearby presence of a mammalian predator. Rat faecal samples were collected from the University of Canterbury Psychology Department lab rats which are fed rat chow pellet R94 (CRT, Rolleston). Faecal samples in 2011 were collected from three cages, each inhabited by two to three rats. In 2012, samples were taken from five cages with two to three rats per cage. Hedgehog samples used in 2011 were collected from four wild caught hedgehogs from South Island locations (Christchurch, St. Arnaud and Golden Bay). The 2012 faecal samples were collected from two wild caught hedgehogs from the Christchurch area. The faecal samples were then frozen until used in the study. The positive control scent was a perfume ('Very Girl' eau de parfum, Onlyou Cosmetics Co., Ltd., diluted 1:4 in distilled water). The responses of skinks to a novel scent was tested, rather than no scent, to ensure that the animals recognised the predatory scents as a specific threat and that they did not just avoid all scents. Each scent was paired against a negative control, which was a drop of water on filter paper.

Prior to a trial, the skink was briefly removed from the terrarium and a scent placed in one randomly chosen retreat. The presentation order of the three different scents was randomly chosen. The methods differed slightly between 2011 and 2012. In 2011, the scent was placed onto a 1 cm^2 piece of white paper to ensure that the surface area of the stimulus was the same in all treatments. For hedgehog scent, the faeces were smeared onto the paper, while for the rats a single dropping was placed on the paper. An identical piece of paper with a drop of water was placed in the non-treated retreats. In 2012, the scent samples were placed inside a folded 'tortilla' of filter paper to reduce any visual stimuli that differed between treatments. An identical 'tortilla' was placed in the non-treated retreat. As there were no differences between years, I combined all data for further analyses.

To determine whether the size of the odour stimulus was sufficient, I also tested the response of skinks to different amounts of faeces. For 15 glossy brown skinks from Pukerua Bay a single rat faecal pellet or a rat faecal pellet-sized piece of hedgehog faeces was used (referred to as a "normal" stimulus). For the remaining 12 skinks, five rat faecal pellets or the equivalent amount of hedgehog faeces was used (referred to as an "increased" stimulus). Thus the volume of faeces was five times greater in one experiment than the other and this was done to ensure the lack of response at the normal stimulus size was not due to insufficient odour.

Prior to being returned to the terrarium the skink was weighed, to check it had not lost more than 10% of its weight in captivity. None of the skinks had lost weight and all were used in subsequent tests. The skink was then placed along the centre of the wall opposite the retreats and filmed for 12 hours with a Sony Hi8 video-cameras and Sony digital cameras set up 1.5 m over the terrarium. The experiment was repeated with each of the scent treatments, with a 12 hour period in-between to avoid habituation. The wood chips were changed and the terraria and retreats were cleaned with hot water between treatments. The skinks were released back into the area they were collected from after the experiments were completed.

The video tapes were later viewed and I recorded: (1) the time that a skink entered or exited a retreat, (2) the type of retreat it entered (scent, including positive control or negative control), and (3) the duration of time spent in each retreat. I evaluated whether or not the two species of skink avoided the scent of rat or hedgehog by investigating which retreat they entered first, which retreat they entered most frequently, which retreat they occupied the longest, how many times they entered any retreat, and how long they spent in any retreat.

Statistical analyses

Data were analysed using the program R (R Core Team, 2013). The packages 'gdata' (Warnes et al., 2013), 'lme4' (Bates et al., 2013) and 'AICcmodavg' (Mazerolle, 2013) were used. Graphs were created in SPSS16 (SPSS, 2007). I compared ecologically relevant models using Akaike's Information Criterion corrected for small sizes (AICc; Burnham and Anderson, 2002) to investigate the factors affecting: which retreat was entered first, which retreat was entered more often, whether the difference in time spent in scented vs. unscented retreats differed, and whether the total number of entries into any retreat or amount of time spent in a retreat differed between

populations or scent treatments. To examine the factors influencing the type of retreat a skink entered first I used generalised linear mixed-effects models with binomial distributions (scented or unscented retreat). To investigate the factors affecting whether the skinks entered scented or unscented retreats more often I used linear mixed-effects models (lmer) with a Poisson distribution (number of entries into scented retreat, transformed to natural log) as a function of the total number of entries. To determine the factors influencing whether the skink spent more time in the scented or unscented retreat I compared lmer models. The dependent factor was the log of the time spent in scented retreat divided by the time spent in the unscented retreat. To examine which factors affected the total number of times a skink entered any retreat I compared lmer models with a Poisson distribution (total number of entries into either retreat, transformed via its natural log). To investigate which factors affected the total amount of time a skink spent in any retreat I compared lmer models with a Gaussian distribution (total number of seconds spent in either retreat, transformed via its natural log).

For all model comparisons the identity of the individual skink was treated as a random factor. The fixed factors were: the type of scent (hedgehog, rat or perfume), whether mammalian predators were present in the area, the skink species, sex, whether or not the skink had caudal autotomy, and if the scent stimulus was normal or increased. Caudal autotomy was included in my models as it is possible that a skink which has previously lost its tail (e.g. through an encounter with a predator) may have a different response than an individual with an intact tail. The null model and all single factor models were compared as well as ecologically sensible two way and three way models (both additive and interactive).

Results

First retreat entered

There was little difference in whether or not the first retreat entered was scented or unscented. Northern grass skinks from Manaroa and glossy brown skinks from Maud Island entered the scented retreat first 53% of the time, while glossy brown skinks from Pukerua Bay entered the scented retreat first 45% of the time. When investigating which variables best predicted whether a skink entered a scented or unscented retreat first, the top-ranking model based on AICc model selection was the interaction between scent and caudal autotomy (AICc weight = 0.17; Table

5.1). Skinks with caudal autotomy entered the scented retreat first slightly more often (51% of the time) than skinks without caudal autotomy (49% of the time). The null model was a close second (AICc weight = 0.12, ΔAICc = 0.76; Table 5.1), giving little support for this model.

Number of entries into each retreat

There was very little difference in the mean number of times a skink entered the scented retreat compared to the unscented retreat in 12 hours. Northern grass skinks from Manaroa entered scented retreats on average 6.6 times and unscented retreats 7.7 times. Glossy brown skinks from Maud Island entered the scented retreat on average 5.4 times and the unscented retreat 5.1 times. Glossy brown skinks from Pukerua Bay entered the scented retreat on average 4.3 times and the unscented retreat 5.5 times. The null model was the top-ranking model based on AICc model selection (AICc weight = 0.56; Table 5.2).

Amount of time spent in retreats

Glossy brown skinks from Pukerua Bay spent the least amount of time in the scented retreat (46%), followed by northern brown skinks from Manaroa (48%) and glossy brown skinks from Maud Island (57%). The proportion of time a skink spent in the scented retreat compared to the negative control (unscented) retreat was best predicted by the interaction between the presence or absence of mammalian predators and caudal autotomy based on AICc model selection (AICc weight = 0.18; Table 5.3), followed by the interaction between the scent treatment and whether or not that scent was increased (AICc weight = 0.16; Table 5.3), the interaction between the skink species and its sex (AICc weight = 0.10; Table 5.3) and the null model (AICc weight = 0.09, ΔAICc = 1.47; Table 5.3). Skinks from sites with mammalian predators present spent less time in the scented retreat (47%) than those from mammalian predator free Maud Island (53%). Skinks with caudal autotomy also spent less time in the scented retreat (47%) compared to those without caudal autotomy (53%). In addition, female skinks spent less time in the scented retreat (45%) than males (57%). However, given the strength of the null model there is little support for any factors in explaining the amount of time spent in retreats in relation to odour treatment.

Total number of entries

Northern grass skinks from Manaroa entered retreats the most in 12 hours (μ 14.3 times), followed glossy brown skinks from Maud Island (μ 10.6 times) and glossy brown skinks from Pukerua Bay (μ 9.8 times). When exploring which variables best predicted the total number of

times a skink entered a retreat, a model containing the skink species and sex was the top-ranking model based on AICc model selection (AICc weight = 0.24; Table 5.4), followed by sex and increased scent stimulus (AICc weight = 0.20; Table 5.4) and the interaction between species and sex (AICc weight = 0.14; Table 5.4) and the interaction between sex and increased scent stimulus (AICc weight = 0.09; Table 5.4). Due to the strength of the null model (AICc weight = 0.04, ΔAICc = 3.48; Table 5.4) there is weak support for these factors. Glossy brown skinks entered retreats less often, and had less variance in the number of entries, than northern grass skinks (Figure 5.2 A). For both species females entered retreats more often than males, though this pattern is stronger in northern grass skinks (Figure 5.2 B & Figure 5.3 A). Glossy brown skinks from Pukerua Bay entered retreats less often if the scent stimulus was increased (Figure 5.2 C). This is true for both sexes (Figure 5.3 B).

Total amount of time spent in retreats

The species of the skink was the best predicator of how long a skink spent in any retreat based on AICc model selection (AICc weight = 0.56; Table 5.5). The models containing species and sex (AICc weight = 0.09; Table 5.5), species and the presence of caudal autotomy (AICc weight = 0.09; Table 5.5) and scent treatment and species (AICc weight = 0.06, Table 5.5) also have merit. Glossy brown skinks spent more time in retreats, and had a larger variance in the amount of time, than northern grass skinks (Figure 5.4 A). Females spent more time in retreats than males (Figure 5.4 B). Skinks with caudal autotomy spent less time in retreats than those without caudal autotomy (Figure 5.4 C). Skinks spent more time in a retreat when the scented retreat had hedgehog faeces than when the scented retreat had rat faeces or the positive control scent (Figure 5.4 D).

Discussion

Avoidance and attraction to scent

Northern grass and glossy brown skinks do not appear to avoid the scent of rat or hedgehog faeces. No attraction or avoidance behaviour was observed in regards to the first retreat entered, the number of times a skink entered any one retreat, the amount of time a skink spent in any one retreat, or the total number of entries into any retreat. However, there is evidence that some anti-predator behaviours may be present. Both species of skink spent more time overall in retreats

when hedgehog scent was present than when rat or the positive control scent was present. In addition, glossy brown skinks from Pukerua Bay entered retreats fewer times (scented and unscented) when the scent stimulus was increased. These patterns may imply that with perceived increased predation pressure the skinks reduce their activity levels. A number of studies have shown that lizards increase refuge use when perceived predation pressure increases (Martín and López, 1999a, b). This may explain why the skinks spent more time in retreats when hedgehog scent was present. Why this behaviour occurs for hedgehogs scent and not rat scent is unknown. It may be due to: the differences in predation strategies between the two species, hedgehogs being a more significant predator than rats, or the strength of the scent (hedgehog faeces smell stronger than rat faeces; *pers. obs.*). Though increased refuge use with perceived predation pressure could explain the decreased number of entries into retreats seen, as a skink may go into one retreat and stay there for a significant amount of time, the problem arises that one would expect a correlated increase in the total amount of time spent in refuges with increased scent treatment, which was not observed. In contrast, it appears that with increased scent stimulus the skinks reduced time spent in all retreats. Therefore another potential hypothesis is that skinks entered retreats less often because they decreased their activity. It is generally assumed that decreased activity leads to decreased predation, which has been observed in many species (Anholt and Werner, 1995; Heinen, 1994; Kotler et al., 1994; Kotler et al., 1992; Kotler et al., 1991; Laurila et al., 2004; Lima, 1998b; Rahel and Kolar, 1990; Ramcharan and Sprules, 1991; Saarikko, 1992; Sih, 1992). For example, the New Zealand endemic tree wētā (*Hemideina crassidens*), increased its activity levels and amount of time entering and exiting refuges after the eradication of the introduced kiore (*Rattus exulans*) and South Island weka (*Gallirallus australis australis*) from Nukuwaiata Island (Rufaut and Gibbs, 2003); and the water flea (*Daphnia galeata*) decreased activity when exposed to predator infochemicals (Weber and Van Noordwijk, 2002).

As New Zealand skinks evolved with visual avian and reptilian predators, being less active in the presence of increased predation risk may have been a successful strategy (Greene, 1988; Hoare, 2006b; Meyer-Rochow, 1988; Meyer-Rochow and Teh, 1991; Worthy and Holdaway, 2002). A comparison of the behaviour of northern grass skinks to that of the introduced rainbow skink (*Lampropholis delicata*) that evolved with mammalian predators, shows lizard behavioural

patterns to be correlated with their evolutionary experience of mammals (Hoare, 2006a). Northern grass skinks exhibited mostly antipredator-freeze behaviour, whereas the rainbow skink was much more active and showed more escape behaviours (Hoare, 2006a). Such changes in behaviour have also been observed over a much shorter time scale. Duvaucel's geckos that are sympatric with rats are more active and exhibit more escape behaviours than those that have never been in contact with mammalian predators (Hoare et al., 2007c). Freeze behaviours are potentially not an effective anti-predation strategy against rats, hedgehogs and other predators as they hunt primarily on scent cues (Armsworth et al., 2005; King, 2005). Thus, the skinks in my study may be able to recognise the threat of predation via the scent of rat and hedgehog faeces, but respond with an anti-predator behaviour that is not appropriate to the predator species. Decreasing activity may even potentially increase the probability of being caught by a rat or hedgehog because by not moving the skinks make themselves easy to find via olfactory clues. More research investigating other species and populations would be necessary to see whether this is a localised response or whether it is more widespread, and if so how severely this is affecting the skink's probability of being captured by mammalian predators.

There are two possible hypotheses to explain the limited predator avoidance behaviour seen in these skinks. The first is that skinks in New Zealand have not yet had time to evolve anti-predator behaviours towards novel mammalian predators. They have only co-existed with rats for around 1000 – 2000 years (Towns and Daugherty, 1994) and hedgehogs for around 150 years (King, 2005). As the ability of reptiles to detect predators through chemical signals appears to be genetic (Stapley, 2003), and New Zealand species of reptiles are generally slow to reproduce, with an annual mean brood size of three to five young (Barwick, 1959; Patterson and Daugherty, 1990), there simply may have been too few generations for anti-predator behaviours to evolve, even once the appropriate alleles appear. This has also been seen in similar studies. For example wood mice (*Apodemus sylvaticus*) avoid traps treated with the faeces of red fox (*Vulpes vulpes*) and common genet (*Genetta genetta*) which are resident predators, while they did not show any avoidance to traps with faeces from the European pine marten (*Martes martes*), a novel predator (Navarro-Castilla and Barja, 2014). In addition, evolution of anti-predator traits may not be occurring because the native population is not large enough, and does not have the genetic diversity to allow them to respond fast enough to predators that have an immediate and large

impact on population size (Strauss et al., 2006). In these situations there may be no evolutionary response by the natives because predation pressure is so strong that all genotypes are affected by predation (Strauss et al., 2006).

The second hypothesis is that there is currently insufficient selection pressure on the skinks to avoid the scent of these predators. There are advantages and disadvantages to using chemical cues to assess the risk of predation (Abrams, 1994; Lima, 1998b; Lima and Dill, 1990). Unlike direct cues, odour does not necessarily indicate the immediate presence of a predator. Thus, using scent may lead a skink to underestimate the risk if the predator is present, but overestimate the threat if it is not (Abrams, 1994; Cooper, 1994; Lima, 1998b; Lima and Dill, 1990). The value of using chemical cues to detect a predator is also dependent upon the characteristics of the predator (Kats and Dill, 1998). Chemical information on slow moving, territorial or ambush predators would be more useful than that from fast moving or wide ranging predators, such as rats and hedgehogs (Kats and Dill, 1998). For example, Head et al. (2002) found that adult scinicid lizards do not respond to the chemical stimuli of a natural predator that is a wide-ranging active forager. Chemical cues would give little information on its actual location (Head et al., 2002). Likewise, the actively foraging red-throated rainbow skink (*Carlia rubrigularis*) does not respond to the odour of its actively foraging varanid predator, the black headed monitor (*Varanus tristis*) (Lloyd et al., 2009). A similar pattern is seen in the adult warm-temperate water skink (*Eulamprus heatwolei*) (Head et al., 2002). Likewise, no change in the behaviour of the mountain spiny lizard (*Sceloporus jarrovi*), to the scent of the actively foraging Arizona kingsnake (*Lampropeltis pyromelana*) was found (Simon et al., 1981). These studies support the hypothesis that it may not be beneficial to avoid the scent of an actively foraging predator.

In other studies there has been some evidence that actively foraging reptiles are able to identify the odour of actively foraging predators. For example, the whiptail lizard (*Aspidoscelis marmorata*) is able to differentiate between the actively-foraging saurophagous (lizard-eating) common collared lizard (*Crotaphytus collaris*), from which it flees, and three species of sympatric nonsaurophagous lizards (Punzo, 2008). Similar results have been found in the responses of lizards to the odour of their squamate predators (Amo et al., 2004a; Bealor and Krekorian, 2002; Cooper, 1990; Lloyd et al., 2009; Stapley, 2003; Van Damme and Quick, 2001;

Vandamme et al., 1995). The black-throated rainbow skink (*Carlia rostralis*), brown bicarinate rainbow-skink (*C. storri*) (Lloyd et al., 2009), and desert iguana (*Dipsosaurus dorsalis*) (Bealor and Krekorian, 2002), may respond to the scent of an actively foraging predator because of overlap in the characteristics of retreats used by both predators and prey. Another example that contradicts the hypothesis that there is no benefit in using odour to identify actively foraging predators is seen in North American pit vipers (Crotalinae) (Miller and Gutzke, 1999). Vomerolfaction is obligatory for these ambush predators to detect the ophiophagous (snake eating) kingsnake (*Lampropeltis getula*) (Miller and Gutzke, 1999). If the pit vipers vomernasal ducts are sutured they do not assume defensive postures in the presence of the kingsnake (Miller and Gutzke, 1999).

Despite a number of studies that have examined prey avoidance of reptiles to reptilian predator chemical cues (Kats and Dill, 1998), the role of chemoreception in anti-predator behaviours of reptiles to mammalian predators has been neglected (Hoare, 2006b; Hoare et al., 2007b; Kats and Dill, 1998). One of the few studies is on the rattlesnakes *Crotalus cerastes* and *C. viridis oreganus* that have been found to respond to the chemical cues of skunks *Spilogale phenax phenax* with novel defensive postures (Cowles, 1938). Likewise, other snakes have also been found to respond to the scent of mammalian prey (Chiszar et al., 1997; Clark, 2004). The ability of snakes to detect the scent of mammalian predators while a similar ability has not been found in lizards (Hoare, 2006b; Hoare et al., 2007b), may be due to snakes having a more highly developed chemosensory system than other squamate reptiles (Schwenk, 1995).

A recent study by Hoare (2006) also found little evidence that New Zealand lizards, including northern grass and glossy brown skinks, use chemoreception to detect or respond to introduced rats. My study differs from Hoare's (2006) work as she investigated the behavioural response to the scents within the first few minutes, while this study looked at whether or not the skinks avoided the scent over 12 hours. In addition, my study investigated a skink's response to hedgehog scent as well as rat scent. Together, these two studies show that indigenous skinks do not appear to show any strong behavioural response to the scent of mammalian predators, or avoid the scent of these predators when choosing a retreat. This continues to build support for the hypotheses that chemosensory behaviours are not well developed in New Zealand lizards,

especially in regard to novel mammalian predators, and that predation by introduced mammals is different from that of native predators.

The effect of increased scent treatment

Increased scent stimulus initiated a greater behavioural response in glossy brown skinks. This implies that my standard scent treatment, which was used exclusively in the Maud Island glossy brown skink and Manaroa northern grass skink experiments, may not have been enough to initiate an avoidance response. It is possible that these populations would have shown more, or stronger, behavioural responses with a stronger scent treatment. In addition, some species only display anti-predator behaviours when the predator faeces contains the scent of a conspecific (Rosell et al., 2013). This was not taken into account in this study. The rat faeces were collected from lab-bred rats that would never have eaten a skink, and the diet of the hedgehogs is unknown as they were wild caught. These two factors, in conjunction with the ecologically relevant amount of scent for the experiment, should be considered when designing future studies.

The effect of sex

Male and female skinks behaved differently to scent. Female skinks entered more retreats, and spent more time in retreats, than male skinks. Sexual differences in predator avoidance have been observed in animals where one sex is more sensitive to predation than the other (Lima and Dill, 1990). Female skinks may be more vulnerable to predation than male skinks due to being heavier and less agile while pregnant (Bauwens and Thoen, 1981; Shine, 1980; Sinervo et al., 1991), and therefore spend more time hiding from predators in retreats. There has been little research on the sex differences in response to predator scent, and what research has been done shows little differences between the sexes. Male and female Marlborough green geckos (*Naultinus manukanus*) showed no behavioural differences to the scent of tuatara (Hoare et al., 2007b) or rat (Hoare, 2006a). A similar lack of difference was observed in iguanid lizards *Liolaemus nitidus* to the scent of a snake predator (Troncoso-Palacios and Labra, 2012). More research would be needed to understand why female and male skinks responded differently in this study.

Caudal autotomy and predator avoidance behaviour

Skinks with caudal autotomy spent less time in retreats than those without. This is contrary to the expectation that a lizard that had escaped a predation attempt via caudal autotomy would be more cautious and spend more time hiding than a skink with a full tail due to a decreased probability of surviving subsequent predatory encounters (Dial and Fitzpatrick, 1984; Downes and Shine, 2001). Velvet geckos (*Oedura lesueur*) with caudal autotomy did not vary their behaviour towards a predator the broad-headed snake (*Hoplocephalus bungaroides*) (Kelehear and Webb, 2006). This is hypothesised to be because (as is also the case in glossy brown skinks) the tail is not needed for locomotion, and thus predation risk is not substantially increased (Kelehear and Webb, 2006). The reason why glossy brown skinks with caudal autotomy spent less time in retreats than full tailed skinks is not understood and would require further investigation. One hypothesis is that they need to forage more for food to re-grow the tail.

Differences in behaviour between species

Glossy brown skinks entered retreats less often, but spent more time in retreats than northern grass skinks. This shows that there are significant behavioural differences between the two species, and that northern grass skinks may be more active than glossy brown skinks. These behavioural differences may influence how well each species survives in sympatry with introduced mammalian predators. Current knowledge suggests that the northern grass skink populations have declined less than those of the glossy brown skink (Hitchmough et al., 2013). More research into how each species interacts with mammalian predators would be needed to verify this hypothesis.

Future directions

More research is needed to better understand whether indigenous skinks are developing anti-predator behaviours to mammalian predators. This study had very limited repetition due to practical constraints. An expansion of this study with an increased number of sites with and without mammalian predators, and an increased number of species, would help verify these results. In addition, there has been little or no research investigating whether skinks can recognise mammalian predators by sight or sound, what actually happens when a skink meets a mammal predator, and whether anti-predator behaviours can be learned over a skink's lifetime. In addition, it would be worth testing the assumption that there is benefit to avoiding certain odours, and that these benefits outweigh the costs involved. This would involve determining

what the fitness costs are to skinks with increased time spent in retreats, and whether avoiding predator odours significantly reduces predation risk.

Conclusion

This study found limited anti-predator behaviours of glossy brown and northern grass skinks to the experimental presentation of rat and hedgehog odour. Skinks spent more time overall hiding in retreats when hedgehog scent was present than when rat or the positive control scent was present. This suggests that potentially skinks have an anti-predator strategy against hedgehogs in which they spend more time hiding when they can smell a hedgehog. With increased scent stimulus glossy brown skinks from Pukerua Bay reduced their number of entries into retreats. A reduction in activity can be a successful anti-predator strategy in the presence of visual hunters, but not in response to chemosensory predators such as rats and hedgehogs. The finding that female skinks spend more time hiding than males skinks may be due to females being more vulnerable to predators than males, and the differences in behaviours between the two species may indicate different abilities to survive predation by mammalian predators. Why skinks with caudal autotomy spend less time in retreats than those without is unknown. Two hypotheses were suggested to explain the lack of any strong anti-predator responses. Firstly, there may not have been enough time for these species to evolve extensive avoidance behaviours, and secondly, there may be insufficient selection pressure for these behaviours to evolve due to the high efficiently of the alien predators, or because rats and hedgehogs are active foragers and thus scent gives the prey limited information on immediate predation pressure. These findings indicate that indigenous New Zealand skinks have not developed substantial avoidance behaviours to the odour of introduced mammalian predators.

Figures and Tables

Table 5.1: AICc comparison of models used to evaluate variables as predictors of which retreat the skinks entered first when given a choice of a retreat with a scent treatment (rat, hedgehog or positive control) or negative control (unscented). Species = species of skink, IS = increased scent stimulus, Mammals = presence or absence of mammalian predators, CA = caudal autotomy, Scent = scent treatment present (rat, hedgehog or positive control).

Model	K	AICc	ΔAICc	AICc Weight	Cumulative Weight	Log Likelihood
Scent * CA	7	305.34	0.00	0.17	0.17	-145.41
Null	2	306.11	0.76	0.12	0.28	-151.03
Sex	3	306.71	1.37	0.08	0.37	-150.30
Species	3	307.68	2.33	0.05	0.42	-150.78
Mammals * CA	5	307.87	2.53	0.05	0.47	-148.79
CA	3	308.00	2.66	0.04	0.51	-150.95
IS	3	308.00	2.66	0.04	0.56	-150.95
Mammals	3	308.08	2.74	0.04	0.60	-150.98
Scent	4	308.46	3.11	0.04	0.64	-150.14
Sex + CA	4	308.54	3.20	0.03	0.67	-150.18
Species + Sex	4	308.57	3.23	0.03	0.70	-150.19
Sex + IS	4	308.71	3.37	0.03	0.73	-150.26
Mammals + Sex	4	308.76	3.42	0.03	0.77	-150.29
Scent + Sex	5	309.16	3.81	0.03	0.79	-149.44
Species + CA	4	309.41	4.07	0.02	0.81	-150.61
CA + IS	4	309.90	4.56	0.02	0.83	-150.86
Mammals + CA	4	309.99	4.65	0.02	0.85	-150.90
Species * Sex	5	309.99	4.65	0.02	0.86	-149.86
Scent + Species	5	310.07	4.73	0.02	0.88	-149.89
Scent + IS	5	310.41	5.06	0.01	0.89	-150.06
Scent + CA	5	310.41	5.07	0.01	0.91	-150.07
Scent + Mammals	5	310.49	5.14	0.01	0.92	-150.10
Species * CA	5	310.54	5.20	0.01	0.93	-150.13
Mammals * Sex	5	310.58	5.24	0.01	0.94	-150.15
Sex * CA	5	310.63	5.29	0.01	0.95	-150.18
Sex * IS	5	310.78	5.44	0.01	0.97	-150.25
Scent * Mammals * CA	13	311.45	6.11	0.01	0.97	-141.84
Scent * Species	7	311.57	6.23	0.01	0.98	-148.52
CA * IS	5	311.77	6.43	0.01	0.99	-150.74
Scent + Mammals + CA	6	312.46	7.11	0.00	0.99	-150.03
Scent * Sex	7	313.39	8.05	0.00	1.00	-149.43
Scent * Mammals	7	313.81	8.46	0.00	1.00	-149.64
Scent * IS	7	314.38	9.04	0.00	1.00	-149.92

Table 5.2: AICc comparison of models used to evaluate variables as predictors of which retreat the skinks entered most often when given a choice of a retreat with a scent treatment (rat, hedgehog or positive control) or negative control (unscented). Species = species of skink, IS = increased scent stimulus, Mammals = presence or absence of mammalian predators, CA = caudal autotomy, Scent = scent treatment present (rat, hedgehog or positive control).

Model	K	AICc	ΔAICc	AICc Weight	Cumulative Weight	Log Likelihood
Null	4	373.87	0.00	0.56	0.56	-182.83
IS	5	377.19	3.32	0.11	0.67	-183.45
Mammals	5	378.18	4.32	0.07	0.73	-183.94
Species	5	378.23	4.36	0.06	0.80	-183.97
CA	5	378.66	4.79	0.05	0.85	-184.18
Sex	5	378.89	5.02	0.05	0.89	-184.29
Scent	6	380.55	6.68	0.02	0.91	-184.06
Sex + IS	6	382.02	8.15	0.01	0.92	-184.80
CA + IS	6	382.06	8.19	0.01	0.93	-184.82
Sex * CA	7	382.24	8.37	0.01	0.94	-183.83
CA * IS	7	382.81	8.94	0.01	0.95	-184.12
Species + Sex	6	382.87	9.00	0.01	0.95	-185.22
Mammals + CA	6	382.96	9.09	0.01	0.96	-185.27
Species + CA	6	383.22	9.35	0.01	0.97	-185.40
Mammals + Sex	6	383.28	9.41	0.01	0.97	-185.43
Sex + CA	6	383.60	9.73	0.00	0.98	-185.59
Sex * IS	7	383.70	9.83	0.00	0.98	-184.57
Scent + IS	7	383.95	10.09	0.00	0.98	-184.69
Species + CA	7	384.66	10.79	0.00	0.99	-185.05
Scent + Species	7	384.95	11.08	0.00	0.99	-185.19
Scent + Mammals	7	384.96	11.09	0.00	0.99	-185.19
Species * Sex	7	385.38	11.51	0.00	0.99	-185.40
Scent + CA	7	385.41	11.54	0.00	0.99	-185.42
Scent + Sex	7	385.61	11.74	0.00	1.00	-185.52
Mammals * CA	7	385.69	11.82	0.00	1.00	-185.56
Scent * IS	9	386.14	12.27	0.00	1.00	-183.60
Mammals * Sex	7	387.04	13.18	0.00	1.00	-186.24
Scent * Mammals	9	387.88	14.01	0.00	1.00	-184.47
Scent * CA	9	388.46	14.59	0.00	1.00	-184.77
Scent + Mammals + CA	8	389.81	15.94	0.00	1.00	-186.53
Scent * Species	9	391.43	17.56	0.00	1.00	-186.25
Scent * Sex	9	392.78	18.91	0.00	1.00	-186.93
Scent * Mammals * CA	15	402.65	28.78	0.00	1.00	-185.05

Table 5.3: AICc comparison of models used to evaluate variables as predictors of which retreat the skinks spent the most time in given a choice of a retreat with a scent treatment (rat, hedgehog or positive control) or negative control (no scent). Species = species of skink, IS = increased scent stimulus, Mammals = presence or absence of mammalian predators, CA = caudal autotomy, Scent = scent treatment present (rat, hedgehog or positive control). Data were normalised by natural log transformation.

Model	K	AICc	ΔAICc	AICc Weight	Cumulative Weight	Residual Log Likelihood
Mammals * CA	6	780.41	0.00	0.18	0.18	-383.97
Scent * IS	8	780.63	0.21	0.16	0.34	-381.90
Species * Sex	6	781.68	1.26	0.10	0.43	-384.60
Null	3	781.88	1.47	0.09	0.52	-387.87
Mammals	4	782.75	2.34	0.06	0.58	-387.26
IS	4	783.36	2.95	0.04	0.62	-387.57
CA * IS	6	783.43	3.02	0.04	0.66	-385.48
Sex	4	783.72	3.31	0.03	0.69	-387.75
Sex * IS	6	784.18	3.76	0.03	0.72	-385.85
Species	4	784.24	3.82	0.03	0.74	-388.01
CA	4	784.31	3.90	0.03	0.77	-388.05
Scent	5	784.64	4.22	0.02	0.79	-387.15
Mammals + Sex	5	784.82	4.40	0.02	0.81	-387.24
Secnt * Mammals * CA	14	784.92	4.50	0.02	0.83	-377.22
Sex + IS	5	785.17	4.76	0.02	0.85	-387.42
Mammals + CA	5	785.23	4.81	0.02	0.86	-387.45
Scent + Mammals	6	785.65	5.24	0.01	0.88	-386.59
CA + IS	5	785.80	5.39	0.01	0.89	-387.73
Mammals * Sex	6	785.83	5.42	0.01	0.90	-386.68
Species + Sex	5	786.14	5.72	0.01	0.91	-387.90
Scent + IS	6	786.17	5.76	0.01	0.92	-386.85
Sex + CA	5	786.21	5.79	0.01	0.93	-387.93
Sex * CA	6	786.39	5.97	0.01	0.94	-386.96
Scent * Mammals	8	786.52	6.11	0.01	0.95	-384.85
Scent + Sex	6	786.54	6.13	0.01	0.96	-387.03
Species + CA	5	786.67	6.25	0.01	0.96	-388.17
Scent + CA	6	787.04	6.62	0.01	0.97	-387.28
Scent * Species	8	787.05	6.64	0.01	0.98	-385.11
Scent + Species	6	787.07	6.66	0.01	0.98	-387.30
Scent * Sex	8	787.65	7.23	0.00	0.99	-385.41
Species * CA	6	787.71	7.30	0.00	0.99	-387.62
Scent + Mammals + CA	7	788.10	7.69	0.00	1.00	-386.73
Scent * CA	8	788.20	7.78	0.00	1.00	-385.69

Table 5.4: AICc comparison of models used to evaluate variables as predictors of how many times a skink entered any retreat. Species = species of skink, IS = increased scent stimulus, Mammals = presence or absence of mammalian predators, CA = caudal autotomy, Scent = scent treatment present (rat, hedgehog or positive control). Data were normalised by natural log transformation.

Model	K	AICc	ΔAICc	AICc Weight	Cumulative Weight	Residual Log Likelihood
Species + Sex	5	486.55	0.00	0.24	0.24	-238.14
Sex + IS	5	486.90	0.35	0.20	0.45	-238.31
Species * Sex	6	487.63	1.08	0.14	0.59	-237.62
Sex * IS	6	488.56	2.01	0.09	0.68	-238.08
IS	4	488.58	2.02	0.09	0.77	-240.20
Species	4	489.34	2.78	0.06	0.83	-240.57
Sex	4	489.70	3.14	0.05	0.88	-240.76
Null	3	490.04	3.48	0.04	0.92	-241.96
CA + IS	5	492.30	5.75	0.01	0.93	-241.01
Sex + CA	5	493.00	6.45	0.01	0.94	-241.36
Mammals	4	493.05	6.50	0.01	0.95	-242.43
Mammals + Sex	5	493.14	6.59	0.01	0.96	-241.43
Species + CA	5	493.44	6.88	0.01	0.97	-241.58
CA	4	493.57	7.02	0.01	0.98	-242.69
CA * IS	6	494.45	7.89	0.00	0.98	-241.03
Mammals * Sex	6	495.26	8.71	0.00	0.99	-241.43
Sex * CA	6	495.59	9.04	0.00	0.99	-241.60
Species * CA	6	496.15	9.59	0.00	0.99	-241.88
Scent * IS	8	496.32	9.77	0.00	0.99	-239.82
Scent + IS	6	496.48	9.92	0.00	0.99	-242.04
Mammals + CA	5	496.61	10.06	0.00	1.00	-243.16
Scent + Species	6	497.21	10.66	0.00	1.00	-242.41
Scent + Sex	6	497.53	10.98	0.00	1.00	-242.57
Scent	5	497.87	11.32	0.00	1.00	-243.80
Mammals * CA	6	498.68	12.13	0.00	1.00	-243.14
Scent * Species	8	499.30	12.74	0.00	1.00	-241.31
Scent + Mammals	6	500.90	14.35	0.00	1.00	-244.25
Scent + CA	6	501.41	14.86	0.00	1.00	-244.51
Scent + Mammals + CA	7	504.47	17.91	0.00	1.00	-244.97
Scent * Sex	8	504.50	17.95	0.00	1.00	-243.91
Scent * Mammals	8	506.20	19.65	0.00	1.00	-244.76
Scent * CA	8	508.24	21.68	0.00	1.00	-245.77
Scent * Mammals * CA	14	515.43	28.87	0.00	1.00	-242.68

Table 5.5: AICc comparison of models used to evaluate variables as predictors of how much time a skink spent in any retreat. Species = species of skink, IS = increased scent stimulus, Mammals = presence or absence of mammalian predators, CA = caudal autotomy, Scent = scent treatment present (rat, hedgehog or positive control). Data were normalised by natural log transformation.

Model	K	AICc	ΔAICc	AICc Weight	Cumulative Weight	Residual Log Likelihood
Species	4	634.44	0.00	0.56	0.56	-313.13
Species + Sex	5	638.01	3.57	0.09	0.66	-313.86
Species + CA	5	638.20	3.76	0.09	0.74	-313.96
Scent + Species	6	638.77	4.33	0.06	0.81	-313.19
Species * CA	6	639.28	4.84	0.05	0.86	-313.44
Species * Sex	6	639.56	5.12	0.04	0.90	-313.58
IS	4	639.63	5.19	0.04	0.94	-315.72
CA * IS	6	641.92	7.48	0.01	0.96	-314.76
CA + IS	5	642.47	8.03	0.01	0.97	-316.09
Sex + IS	5	642.63	8.20	0.01	0.98	-316.18
Scent * IS	8	643.40	8.96	0.01	0.98	-313.36
Scent + IS	6	643.65	9.21	0.01	0.99	-315.62
Sex * IS	6	644.05	9.62	0.00	0.99	-315.83
Scent * Species	8	644.27	9.83	0.00	1.00	-313.79
Null	3	646.33	11.90	0.00	1.00	-320.11
Sex	4	648.72	14.29	0.00	1.00	-320.27
CA	4	648.87	14.43	0.00	1.00	-320.34
Mammals	4	649.33	14.89	0.00	1.00	-320.57
Scent	5	650.50	16.06	0.00	1.00	-320.11
Sex + CA	5	651.42	16.99	0.00	1.00	-320.57
Mammals + CA	5	651.88	17.44	0.00	1.00	-320.80
Mammals + Sex	5	651.89	17.45	0.00	1.00	-320.80
Scent + Sex	6	652.82	18.39	0.00	1.00	-320.21
Scent + CA	6	653.13	18.69	0.00	1.00	-320.36
Mammals * CA	6	653.46	19.02	0.00	1.00	-320.53
Scent + Mammals	6	653.46	19.03	0.00	1.00	-320.53
Sex * CA	6	653.52	19.08	0.00	1.00	-320.56
Mammals * Sex	6	653.68	19.24	0.00	1.00	-320.64
Scent + Mammals + CA	7	656.11	21.68	0.00	1.00	-320.79
Scent * Sex	8	657.48	23.04	0.00	1.00	-320.39
Scent * Mammals	8	657.65	23.21	0.00	1.00	-320.48
Scent * CA	8	658.32	23.88	0.00	1.00	-320.82
Scent * Mammals * CA	14	666.32	31.88	0.00	1.00	-318.12

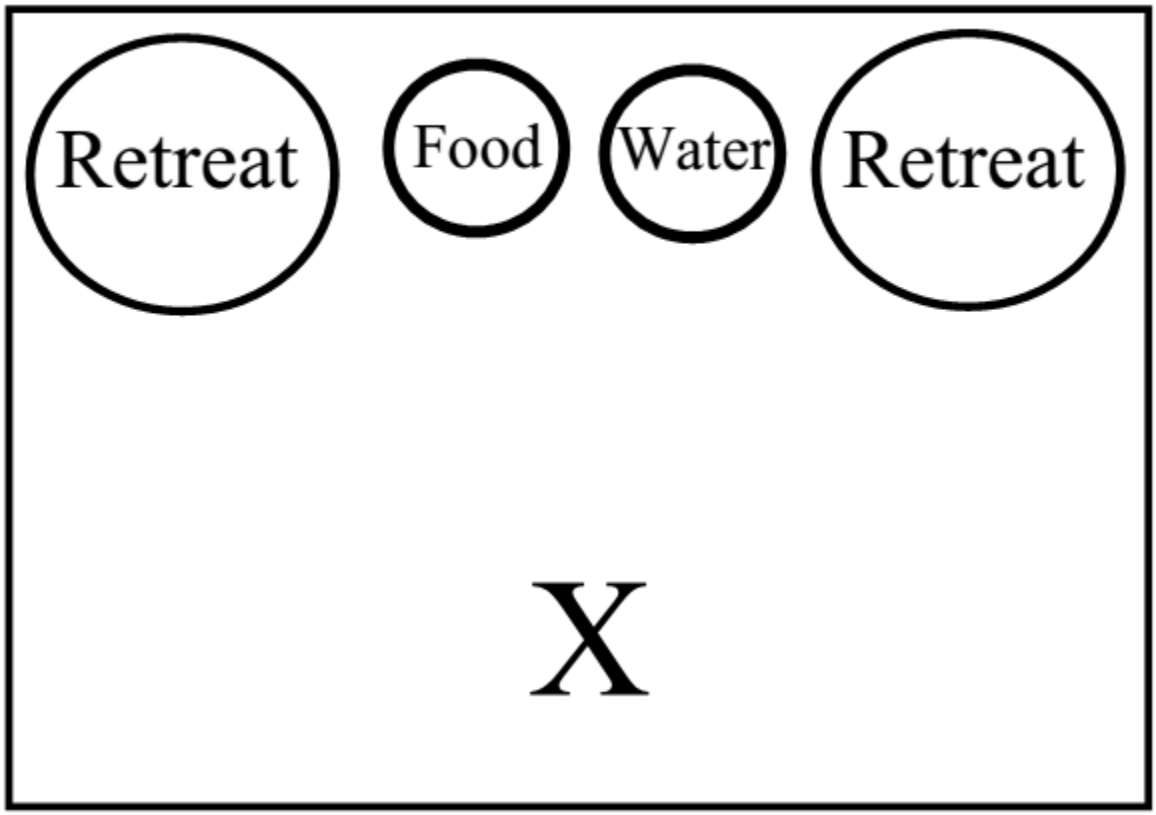

Figure 5.1: Diagram of the terrarium used to test the responses of skinks to the odour of two potential mammalian predators. The terrarium was a 58 cm x 43 cm x 28 cm black plastic tub. Retreats were plastic potting containers, 10 cm deep, 8 cm diameter, turned upside down with a thumb-sized hole cut in the bottom for an entrance. Food containers were small plastic petri dishes. The X represents the location the release point of the skink after the scents were added to the retreats.

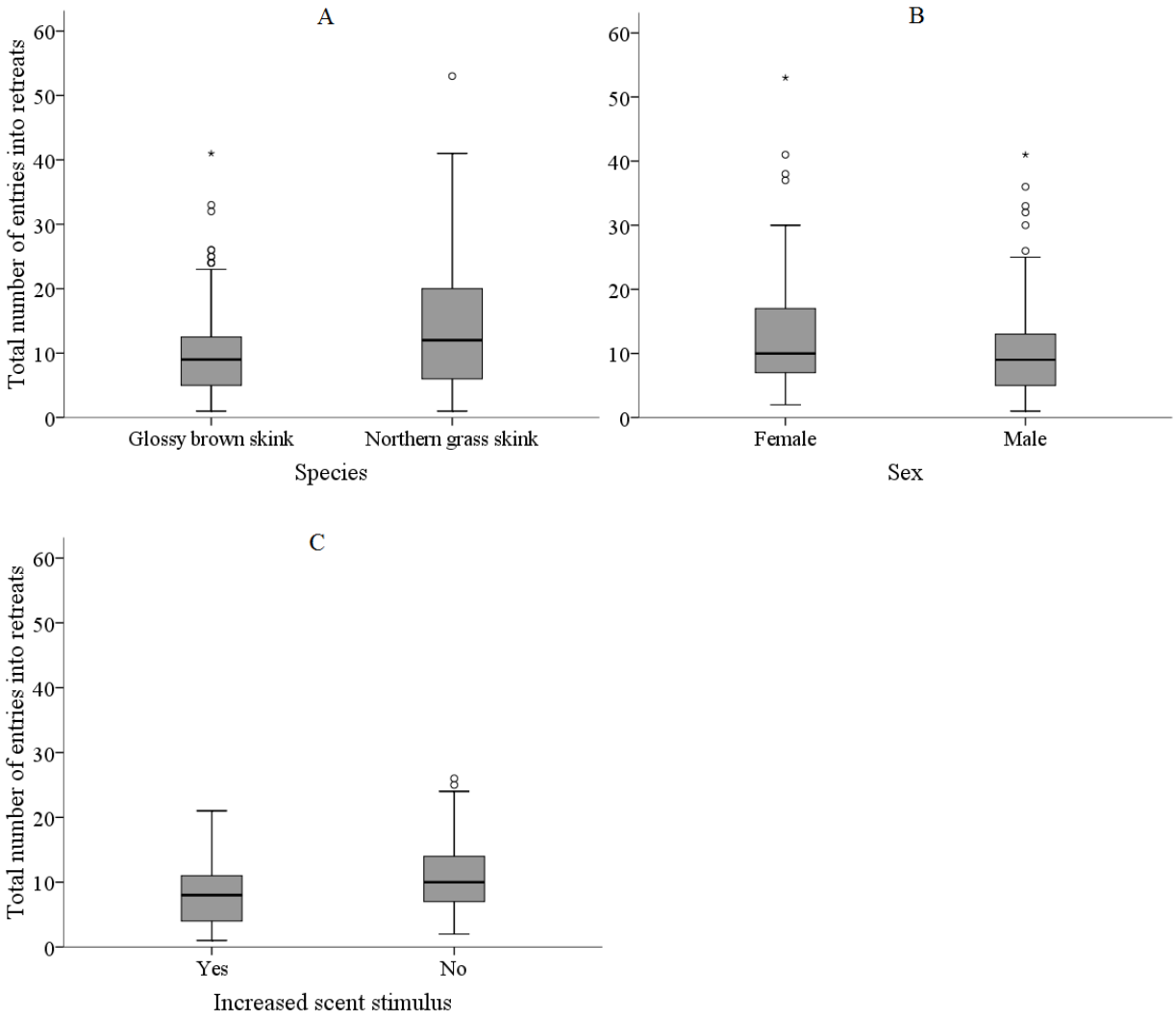

Figure 5.2: A comparison of the total number of times a skink entered any retreat in relation to: (A) species, (B) sex and (C) increased scent stimulus. Graph (C) only uses data from Pukerua Bay glossy brown skinks. The dark horizontal line is the median. The upper edge of each box is the upper quartile and the lower edge of each box is the lower quartile. The whiskers include 95% of the data. Open circles represent outliers, and * represent extreme outliers.

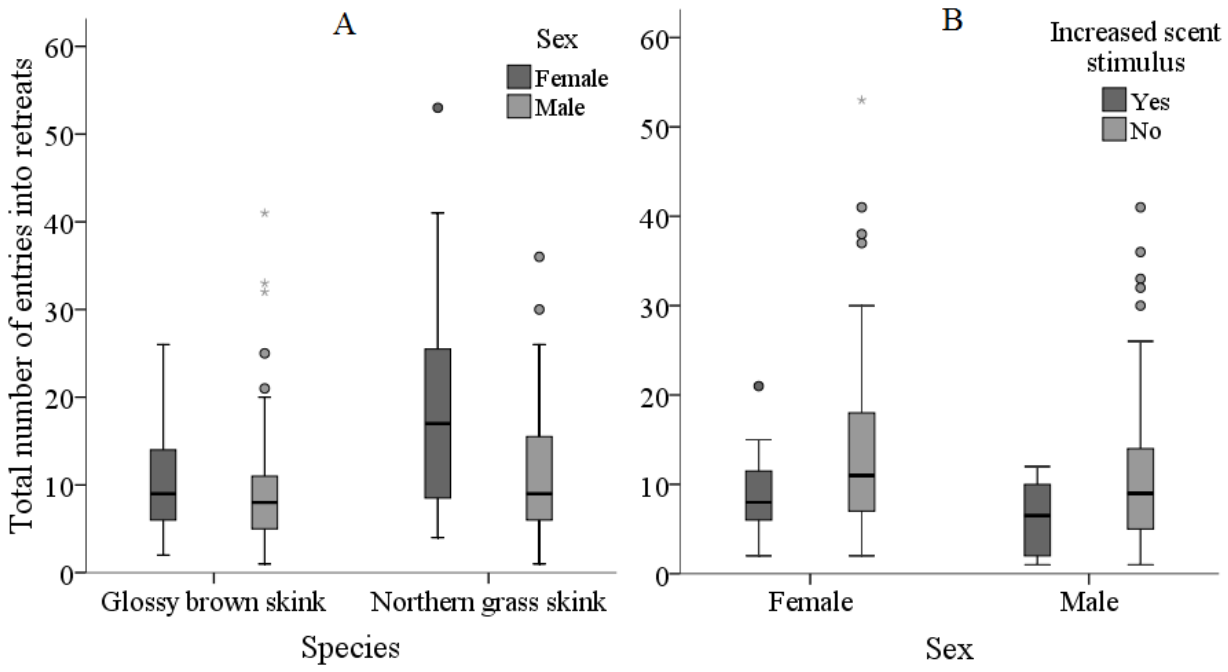

Figure 5.3: A comparison of the total number of times a skink entered any retreat in relation to (A) species and sex and (B) sex and increased scent stimulus (glossy brown Pukerua Bay skinks only). The dark horizontal line is the median. The upper edge of each box is the upper quartile and the lower edge of each box is the lower quartile. The whiskers include 95% of the data. Open circles represent outliers, and * represent extreme outliers.

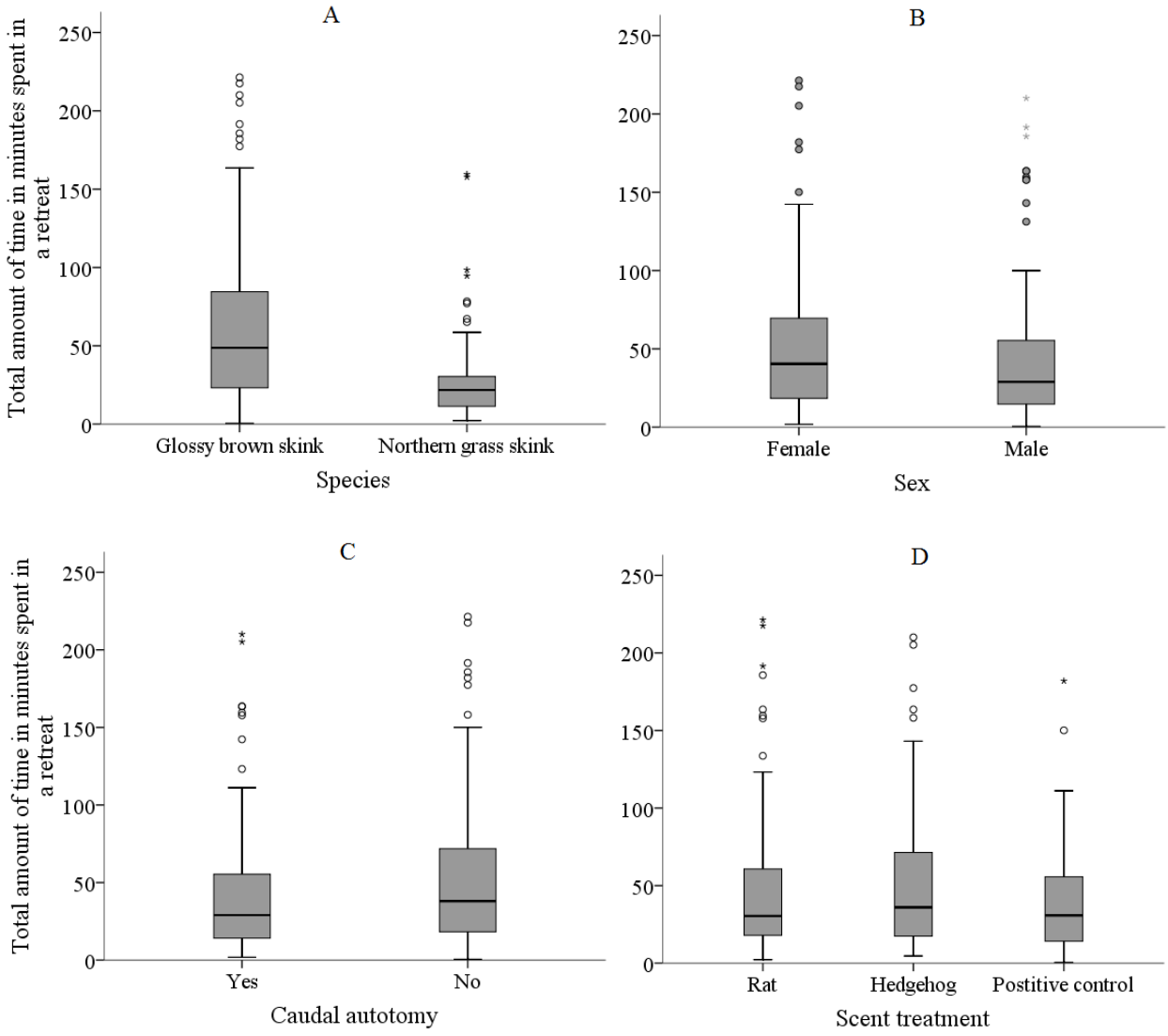

Figure 5.4: A comparison of the total amount of time in minutes a skink spent in any retreat in relation to: (A) species, (B) sex, (C) presence or absence of caudal autotomy, and (D) the scent treatment. The dark horizontal line is the median. The upper edge of each box is the upper quartile and the lower edge of each box is the lower quartile. The whiskers include 95% of the data. Open circles represent outliers, and * represent extreme outliers. Two outliers were removed from this graph for ease of visual presentation. They were a skink from Manaroa who spent 480 minutes in a retreat and a skink from Pukerua bay that spent 609 minutes in a retreat.

Chapter 6: General discussion, conservation implications and directions for future research

Introduced species are a worldwide problem and may soon surpass habitat loss as the main cause of global environmental degradation (Chapin III et al., 2000). New Zealand provides an excellent example of the effect of exotic predators on native populations. For many million years prior to human contact 1250-1300 years ago (Anderson, 1991; Wilmshurst and Higham, 2004), there were no terrestrial mammals present (Worthy et al., 2006), except for three species of bat (Anderson, 1996; Holdaway, 1996; Worthy and Holdaway, 2002). Since then 11 mammalian predators have been introduced, more than any other archipelago (Towns et al., 1997). This has had a substantial impact on the native fauna, including the reptiles (Worthy and Holdaway, 2002). This study has furthered our understanding of the effects of introduced mammalian predators on indigenous skink populations (Table 6.1). It has added to basic knowledge on the life history traits and ecology of some of the less studied skink species (Chapter 2), assessed the effectiveness of mammalian predator control in conserving skink populations (Chapter 3), explored long term trends in a skink community over 17 years (Chapter 3), investigated potential sub-lethal effects of mammalian predators (Chapter 4), and tested the ability of two skink species to avoid the scent of rat or hedgehog, two of the major introduced predators (Chapter 5).

Lizard populations are in decline on the New Zealand mainland (Hitchmough et al., 2013). My research confirms this continuing decline in several species of skinks. The abundance of all skink species at Lake Station appears to have declined dramatically since 1995, especially for the nationally rare speckled and spotted skinks (Chapter 3). In addition, since the 1970's the proportion of female northern grass skinks and larger individuals of both sexes caught at Lake Station has decreased, suggesting females and larger individuals are more vulnerable to predation (Chapter 2). Even within the predator-controlled area of the Rotoiti Nature Recovery Project (RNRP) the skink populations are in serious decline, with the larger and rarer speckled skink near extirpation (Chapter 3). This evidence, in conjunction with the finding that the number of predators trapped has not declined significantly since the implementation of predator control (Chapter 3), suggests that the level of predator control needed to protect these indigenous species is quite high, and higher than that used at present. This is supported by other research

which found only complete or intensive mammalian predator removal resulted in lizard population growth (Reardon et al., 2012; Wilson, 2007). Thus, for the continued survival of indigenous reptile populations on the mainland, especially for larger, ground foraging species, intensive mammalian predator control or the creation of invasive predator-free 'mainland islands' appears necessary. For the continued existence and recovery of skink populations in the RNRP I recommend substantially increasing mammalian predator control within and around skink habitat. In addition, once intensive predator control is in place and proves effective with the northern grass skink population, re-introduction of speckled and spotted skinks from larger populations may be necessary to reduce Allee effects, minimise inbreeding, and increase the population size to facilitate the remaining skinks being able to find each other to breed. In addition, I recommend an investigation into the feasibility of mammalian predator control or exclusion at Lake Station. Spencer et al. (1998) and Efford et al. (unpubl. data) have used the area for many years due to it being good habitat and hosting a large population of spotted, speckled and northern grass skinks. This is no longer the case (Chapter 2 & 3). It may however, be an excellent location to focus conservation efforts.

Northern grass and glossy brown skinks appear to be experiencing sub-lethal predation effects. Body condition was significantly lower in areas with mammalian predators present than without. This has serious conservation implications because it shows that lizard populations may not only be in decline from direct predation, but also additional stresses associated with that predation that may lead to reduced reproductive output. In addition, in areas with mammalian predators present, northern grass skinks with caudal autotomy had higher body condition than those without. This suggests the possibly that skinks with higher body condition are more likely to escape a predator via caudal autotomy. These findings suggest that through habitat manipulation (Sinclair et al., 1998; Souter et al., 2004) it may be possible to decrease the lethal and sub-lethal effects of predation by mammalian predators.

Due to the strong ecological effects of exotic predators on native species, alien predators can cause evolutionary changes in their prey, allowing some native species to co-exist (Strauss et al., 2006). Co-evolution of indigenous species to introduced predators has been found in many species (Bell, 2002; Kiesecker and Blaustein, 1997; Kovacs et al., 2012; Mella et al., 2014;

Parsons and Blumstein, 2010; Strauss et al., 2006) including some in New Zealand (Bremner et al., 1989; Massaro et al., 2008; Rufaut and Gibbs, 2003). Of particular relevance to this thesis is the predator avoidance behaviour found in the Duvaucel's geckos (*Hoplodactylus duvaucelii*) and other lizards (Hoare et al., 2007c). In contrast, this study found no evidence of strong, ecologically successful, avoidance behaviours in glossy brown and northern grass skinks to the experimental presentation of rat and hedgehog odour (Chapter 5). Two hypotheses were suggested to explain this. Firstly, there may not have been enough time for these species to evolve extensive avoidance behaviours, and secondly, there may be insufficient selection pressure for these behaviours to evolve as rats and hedgehogs are active foragers and thus scent gives the prey limited information on immediate predation pressure. This lack of evidence for the evolution of anti-predator behaviour, in conjunction with the results of the other chapters, highlights the importance of mammalian predator control for the continued survival of these species on the mainland.

Future research directions

My work has generated a number of avenues for further research into the life history of New Zealand lizard species, how to increase the effectiveness of mammalian predator control to revitalise lizard populations, the sub-lethal effects of alien predators on native prey and the abilities of naïve prey to respond to novel predators. These research opportunities have both theoretical and conservation implications. I specifically recommend research into the following:

1. *Increase the knowledge of the life history traits and ecology of New Zealand's lizard species*. For many species there are substantial gaps in our knowledge. Information on the life history and ecology of a species is vital in creating well-designed conservation initiatives as it allows managers to tailor efforts in accordance with species-specific ecological factors, such as the timing of breeding seasons and behavioural differences between species. It also allows managers to identify demographic changes over time and between areas, which may indicate problems within the population, or show the success of the conservation efforts. In addition, it can improve future research.
2. *Further research into the effects of detrimental sub-lethal predation effects on New Zealand lizards.* This research found that the body condition of northern grass and glossy

brown skinks were significantly lower in populations with mammalian predators present than those without. This has been found in one other lizard species in New Zealand (Christmas, 1995). Due to the conservation implications of decreased fitness through reduced body condition, I highly recommended further investigation into other species and populations to see if this is a widespread pattern. I also suggest direct investigation into the degree decreased body condition affects the long and short-term fitness of New Zealand lizards.

3. *Research into increasing survival and/or reproduction rates of lizards through habitat manipulation, increased food or refuge sources.* If successful, such conservation initiatives could allow skink populations to increase without needing to decrease predator numbers to as great an extent (Sinclair et al., 1998; Souter et al., 2004). To date such projects have not proved successful in New Zealand (Lettink et al., 2010), but the research has been minimal. This has potential to apply to Resource Management Act cases in which lizard management often involves salvage of important populations of threatened species and moving them into new habitat, which in many cases has been modified.
4. *Broader research into whether or not native lizards are evolving anti-predator responses to introduced predators.* There has been little research investigating whether skinks can recognise mammal predators by sight or sound, what actually happens when a skink meets a mammal predator, and whether anti-predator behaviours can be learned over a skink's lifetime. Answering these questions is important to understanding whether or not New Zealand's lizards are co-evolving with the introduced predators, and if so, the conservation implications of this process.

Conclusion

In contrast to birds, New Zealand's reptiles have generally not attracted the same level of attention by researchers and conservationists, nor the same level of resources for their preservation (Wilson, 2004). This is unfortunate, as the reptiles of New Zealand provide a superb example of adaptive radiation, rivalling and even exceeding that of the more famous Galapagos finches, with species of reptiles in almost every habitat and altitude in the country (Daugherty et al., 1994). Furthermore, their roles in ecosystem functioning are only now becoming apparent,

with some species important in pollination and seed dispersal services (Olesen and Valido, 2003; Whitaker, 1987). Unlike birds, which typically require large territories (and thus large areas of predator control for their survival), the per capita cost of conserving a skink or gecko is likely to be minimal as many spend their entire lives within tens of square metres (Barwick, 1959; Turner et al., 1969). Thus it should be possible to protect relatively large populations of every endangered species of reptile in New Zealand at a fraction of the cost currently devoted to iconic birds such as kakapo or kiwi. This does not deny the importance of conserving birds but nor should reptiles be sacrificed because they are less iconic. Although there was some hope that conservation efforts for birds would prove beneficial to reptiles at the same time (i.e., the RNRP), my work suggests this is not the case. Reptile conservation needs to be a primary goal in its own right, and not a secondary thought, or otherwise we risk losing all but a few of the hardiest species (Towns et al., 2001).

Table

Table 6.1: Summary of thesis research questions and the answers that could be provided.

Research Question	Results from this thesis	Chapter
Increase the basic knowledge of the life history traits of common, spotted and speckled skinks.	• I estimated the size at sexual maturity and breeding season for speckled skinks. • The months that skinks were trapped the most often in is species specific. • Speckled skinks preferred shrub habitat with rocks present. • Since the 1970's the proportion of female northern grass skinks caught at Lake Station has decreased. • Since the 1970's the proportion of larger northern grass skinks caught at Lake Station has decreased.	Chapter 2
Are the indigenous skink populations increasing within the Rotoiti Nature Recovery Project (RNRP) in Nelson Lakes National Park following mammalian predator control implemented in 2001?	• The level of mammalian predator control occurring in the RNRP is insufficient to protect or to allow for the recovery of the indigenous skink populations. • The northern grass and speckled skink populations within the RNRP have decreased significantly between 2002 and 2012, with the speckled population near local extinction.	Chapter 3
Have the skink population demographics at Lake Station changed significantly since 1995?	• The abundance of all skink species at Lake Station appears to have declined dramatically since 1995, especially for the nationally rare speckled and spotted skinks.	
Are introduced mammalian predators causing substantial sub-lethal fitness effects on indigenous skink populations?	• For both species body condition was lower in populations with mammalian predators present. • For northern grass skinks in areas with mammalian predators present, skinks with caudal autotomy had higher body condition than those without. • Caudal autotomy was more common in the absence of mammalian predators. • The presence of mammalian predators had little effect on the parasitic chigger mite load.	Chapter 4
Do the indigenous New Zealand glossy brown and northern grass skinks have the ability to detect and avoid the faecal scent of two introduced mammalian predators (ship rat and hedgehog)?	• There was little evidence of avoidance or attraction behaviours of either species to the experimental presentation of rat and hedgehog odour. • With increased scent stimulus skinks decreased their number of entries into retreats. • Skinks spent more time hiding in retreats when hedgehog scent was present than when rat or the positive control scent was present. • Females entered retreats more often and spent more time in retreats than males. • Glossy brown skinks entered retreats less often and spent more time in retreats than northern grass skinks. • Skinks with caudal autotomy spent less time in retreats than those without.	Chapter 5

References

Abrams, P.A. 1994. Should prey overestimate the risk of predation? *The American Naturalist 144*: 317-328.

Aeschlimann, A. 1991. Ticks and disease: susceptible hosts, reservoir hosts, and vectors. *Parasite-host associations: resistance or conflict*: 148-156.

Allen, C.R.; Rice, K.G.; Wojcik, D.P.; Percival, H.F. 1997. Effect of red imported fire ant envenomization on neonatal American alligators. *Journal of Herpetology 31*: 318-321.

Amo, L.; López, P.; Martı´n, J. 2006. Nature-based tourism as a form of predation risk affects body condition and health state of *Podarcis muralis* lizards. *Biological Conservation 131*: 402-409.

Amo, L.; Lopez, P.; Martin, J. 2007a. Habitat deterioration affects body condition of lizards: A behavioral approach with *Iberolacerta cyreni* lizards inhabiting ski resorts. *Biological Conservation 135*: 77-85.

Amo, L.; Lopez, P.; Martin, J. 2007b. Refuge use: A conflict between avoiding predation and losing mass in lizards. *Physiology & Behavior 90*: 334-343.

Amo, L.; López, P.; Martín, J. 2004a. Chemosensory recognition and behavioral responses of wall lizards, *Podarcis muralis*, to scents of snakes that pose different risks of predation. *Copeia, 2004*: 691-696.

Amo, L.; López, P.; Martín, J. 2004b. Prevalence and intensity of haemogregarinid blood parasites in a population of the Iberian rock lizard, *Lacerta monticola*. *Parasitology research 94*: 290-293.

Anderson, A. 1991. The chronology of colonization in New Zealand. *Antiquity 65*: 767-795.

Anderson, A. 1996. Was "*Rattus exulans*" in New Zealand 2000 Years Ago? AMS Radiocarbon Ages from Shag River Mouth. *Archaeology in Oceania*: 178-184.

Andren, C.; Nilson, G. 1983. Reproductive tactics in an island population of adders, *Vipera berus* (L.), with a fluctuating food resource. *Amphibia-Reptilia 4*: 63-79.

Anholt, B.R.; Werner, E.E. 1995. Interaction between food availability and predation mortality mediated by adaptive-behavior. *Ecology 76*: 2230-2234.

Armsworth, C.; Bohan, D.; Powers, S.; Glen, D.; Symondson, W. 2005. Behavioural responses by slugs to chemicals from a generalist predator. *Animal Behaviour 69*: 805-811.

Arnold, E. 1984. Evolutionary aspects of tail shedding in lizards and their relatives. *Journal of Natural History 18*: 127-169.

Atkins, N.M., Wapstra, E. 2004. Successful treatment of mite infestastion in gravid spotted snow skinks (*Niveoscinus ocellatus*). *Herpetofauna 34*: 66-69.

Atkinson, I. 1989. Introduced animals and extinctions. *In:* Western, D.; Pearl, M.C. (Editors), *Conservation for the twenty-first century*, pp 54-75. Oxford University Press, Oxford.

Atkinson, I.A.E.; Moller, H. 1990. Kiore. *In:* King, C. (Editor), *The handbook of New Zealand mammals*, pp 175-192. Oxford University Press, Oxford.

Autumn, K.; De Nardo, D.F. 1995. Behavioral thermoregulation increases growth rate in a nocturnal lizard. *Journal of Herpetology*: 157-162.

Avery, R. 1970. Utilization of caudal fat by hibernating common lizards, *Lacerta vivipara*. *Comparative Biochemistry and Physiology 37*: 119-121.

Avery, R. 1984. Physiological aspects of lizard growth: the role of thermoregulation. *Symposium of the Zoological Society of London.* pp 407-424.

Ballinger, R.E. 1977. Reproductive strategies: food availability as a source of proximal variation in a lizard. *Ecology*: 628-635.

Ballinger, R.E.; Tinkle, D.W. 1979. On the cost of tail regeneration to body growth in lizards. *Journal of Herpetology 13*: 374-375.

Barr, B.P. 2009. Spatial ecology, habitat use, and the impacts of rats on chevron skinks (*Oligosoma homalonotum*) on Great Barrier Island. Msc. Massey University, Auckland.

Barwick, R. 1959. The life history of the common New Zealand skink *Leiolopisma zelandica* (Gray, 1843). *Transactions of the Royal Society of New Zealand 86*: 331-380.

Bateman, P.W.; Fleming, P.A. 2009. To cut a long tail short: a review of lizard caudal autotomy studies carried out over the last 20 years. *Journal of Zoology 277*: 1-14.

Bates, D.; Maechler, M.; Bolker, B. 2013. lme4: Linear mixed-effects models using S4 classes. *R package version 0.999999-2*.

Bauer, A.M.; Russell, A.P. 1986. *Hoplodactylus delcourti* n. sp.(Reptilia: Gekkonidae), the largest known gecko. *New Zealand Journal of Zoology 13*: 141-148.

Bauwens, D.; Thoen, C. 1981. Escape tactics and vulnerability to predation associated with reproduction in the lizard *Lacerta vivipara*. *The Journal of Animal Ecology*: 733-743.

Bealor, M.T.; Krekorian, C.O.N. 2002. Chemosensory identification of lizard-eating snakes in the desert iguana, *Dipsosaurus dorsalis* (Squamata: Iguanidae). *Journal of Herpetology 36*: 9-15.

Bell, B.D. 2002. The eradication of alien mammals from five offshore islands, Mauritius, Indian Ocean. *In:* Veitch, C.R.; Clout, M.N. (Editors), *Turning the tide: the eradication of invasive species*, p 40. IUCN, Gland.

Bellairs, A.A.; Bryant, S. 1985. Autotomy and regeneration in reptiles. *Biology of the Reptilia 15*: 301-410.

Bernardo, J.; Agosta, S.J. 2005. Evolutionary implications of hierarchical impacts of nonlethal injury on reproduction, including maternal effects. *Biological Journal of the Linnean Society 86*: 309-331.

Best, L.W. 1969. Food of the roof-rat, *Rattus rattus rattus* (L.), in two forest areas of New Zealand. *New Zealand journal of science 12*: 258-267.

Bettesworth, D.J. 1972. *Rattus exulans* on Red Mercury Island. *Tane 18*: 117-118.

Bettesworth, D.J.; Anderson, G.R.V. 1972. Diet of *Rattus norvegicus* on Whale Island, Bay of Plenty, New Zealand. *Tane 18*: 189-195.

Blumstein, D.T. 2002. Moving to suburbia: ontogenetic and evolutionary consequences of life on predator-free islands. *Journal of Biogeography 29*: 685-692.

Blumstein, D.T.; Daniel, J.C. 2005. The loss of anti-predator behaviour following isolation on islands. *Proceedings of the Royal Society B: Biological Sciences 272*: 1663.

Blumstein, D.T.; Mari, M.; Daniel, J.C.; Ardron, J.G.; Griffin, A.S.; Evans, C.S. 2002. Olfactory predator recognition: wallabies may have to learn to be wary. *Animal Conservation 5*: 87-93.

Bremner, A.; Barratt, B.; Butcher, C.; Patterson, G. 1989. The effects of mammalian predation on invertebrate behaviour in South West Fiordland. *New Zealand Entomologist 12*: 72-75.

Bull, P.C.; Whitaker, A.H. 1975. V. The amphibians, reptiles, birds and mammals. *In:* Kuschel, G. (Editor), *Biogeography and ecology in New Zealand*, p 231. Springer Netherlands, The Hauge.

Burnham, K.P.; Anderson, D.R. 2002. *Model selection and inference: A practical information-theoretic approach*. Springer-Verlag, New York.

Camin, J.H. 1948. Mite transmission of a hemorrhagic septicemia in snakes. *The Journal of Parasitology 34*: 345-354.

Carlile, P.A.; Peters, R.A.; Evans, C.S. 2006. Detection of a looming stimulus by the Jacky dragon: selective sensitivity to characteristics of an aerial predator. *Animal Behaviour 72*: 553-562.

Case, T.J.; Bolger, D.T. 1991. The role of introduced species in shaping the distribution and abundance of island reptiles. *Evolutionary Ecology 5*: 272-290.

Case, T.J.; Bolger, D.T.; Richman, A.D. 1998. Reptilian extinctions over the last ten thousand years. *In:* Fiedler, P.L.; Kareiva, P.M. (Editors), *Conservation biology: for the coming decade*, pp 157-186. Chapman & Hall, New York.

Cassels, R. 1984. The role of prehistoric man in the faunal extinctions of New Zealand and other Pacific islands. *In:* Martin, P.S.; Klein, R.G. (Editors), *Quarternary Extinction*. University of Arizona Press, Tuscon.

Chambers, G.K.; Boon, W.M.; Buckley, T.R.; Hitchmough, R.A. 2001. Using molecular methods to understand the Gondwanan affinities of the New Zealand biota: three case studies. *Australian Journal of Botany 49*: 377-387.

Chapin III, F.S.; Zavaleta, E.S.; Eviner, V.T.; Naylor, R.L.; Vitousek, P.M.; Reynolds, H.L.; Hooper, D.U.; Lavorel, S.; Sala, O.E.; Hobbie, S.E. 2000. Consequences of changing biodiversity. *Nature 405*: 234-242.

Chapple, D.G.; McCoull, C.J.; Swain, R. 2002. Changes in reproductive investment following caudal autotomy in viviparous skinks (*Niveoscincus metallicus*): Lipid depletion or energetic diversion? *Journal of Herpetology 36*: 480-486.

Chapple, D.G.; Ritchie, P.A.; Daugherty, C.H. 2009. Origin, diversification, and systematics of the New Zealand skink fauna (Reptilia: Scincidae). *Molecular Phylogenetics and Evolution 52*: 470-487.

Chapple, D.G.; Swain, R. 2004. Inter-populational variation in the cost of autotomy in the metallic skink (*Niveoscincus metallicus*). *Journal of Zoology 264*: 411-418.

Chiszar, D.; Lukas, W.; Smith, H.M. 1997. Response to rodent saliva by two species of rodentiophagous snakes. *Journal of Chemical Ecology 23*: 829-836.

Christian, K.; Baudinette, R.; Pamula, Y. 1997. Energetic costs of activity by lizards in the field. *Functional Ecology 11*: 392-397.

Christmas, E. 1995. Interactions between Duvaucel's gecko (*Hoplodactylus duvaucelii*) and kiore (*Rattus exulans*). *Unpublished MSc Thesis. University of Otago, Dunedin, New Zealand*.

Civantos, E.; Forsman, A. 2000. Determinants of survival in juvenile *Psammodromus algirus* lizards. *Oecologia 124*: 64-72.

Civantos, E.; Lopez, P.; Martin, J. 2010. Non-lethal effects of predators on body growth and health state of juvenile lizards, *Psammdromus algirus*. *Physiology & Behavior 100*: 332-339.

Civantos, E.; Salvador, A.; Veiga, J.P. 1999. Body size and microhabitat affect winter survival of hatchling *Psammodromus algirus* lizards. *Copeia*: 1112-1117.

Clark, R.W. 2004. Timber rattlesnakes (*Crotalus horridus*) use chemical cues to select ambush sites. *Journal of Chemical Ecology 30*: 607-617.

Clobert, J.; Oppliger, A.; Sorci, G.; Ernande, B.; Swallow, J.; Garland, J. 2000. Trade offs in phenotypic traits: endurance at birth, growth, survival, predation and susceptibility to parasitism in a lizard, *Lacerta vivipara*. *Functional Ecology 14*: 675-684.

Clout, M.N.; Veitch, C.R. 2002. Turning the tide of biological invasion: the potential for eradicating invasive species. *Occasional Paper of the IUCN Species Survival Commission*. Iucn.

Cogger, H.G.; Cameron, E.; Sadlier, R.; Eggler, P. 1993. *The action plan for Australian reptiles*. Australian Nature Conservation Agency Canberra, Australia.

Congdon, J.; Vitt, L.; King, W. 1974. Geckos: adaptive significance and energetics of tail autotomy. *New Zealand Herpetology 184*: 1379.

Cooper Jr, W.E. 2000. An adaptive difference in the relationship between foraging mode and responses to prey chemicals in two congeneric scincid lizards. *Ethology 106*: 193-206.

Cooper, W.E. 1990. Chemical-detection of predators by a lizard, the broad-headed skink (*Eumeces laticeps*). *Journal of Experimental Zoology 256*: 162-167.

Cooper, W.E. 1994. Chemical-discrimination by tongue-flicking in lizards - a review with hypotheses on its origin and its ecological and phylogenetic-relationships. *Journal of Chemical Ecology 20*: 439-487.

Cooper, W.E. 2003. Shifted balance of risk and cost after autotomy affects use of cover, escape, activity, and foraging in the keeled earless lizard (*Holbrookia propinqua*). *Behavioral Ecology and Sociobiology 54*: 179-187.

Cooper, W.E.; Wilson, D.S. 2008. How to stay alive after losing your tail. *Behaviour 145*: 1085-1099.

Coss, R.G. 1999. Effects of relaxed natural selection on the evolution of behavior. *Geographic variation in behavior: Perspectives on evolutionary mechanisms*: 180-208.

Cowles, R.B. 1938. Unusual defense postures assumed by rattlesnakes. *Copeia 1938*: 13-16.

Cree, A. 1994. Low annual reproductive output in female reptiles from New Zealand. *New Zealand Journal of Zoology 21*: 351-372.

Cree, A.; Daugherty, C.H.; Hay, J.M. 1995. Reproduction of a rare New-Zealand reptile, the tuatara *Sphenodon punctatus*, on rat-free and rat-inhabited Islands. *Conservation Biology 9*: 373-383.

Cree, A.; Guillette Jr, L.J. 1995. Biennial reproduction with a fourteen-month pregnancy in the gecko *Hoplodactylus maculatus* from southern New Zealand. *Journal of Herpetology 29*: 163-173.

Crook, I.G. 1973. The tuatara, *Sphenodon punctatus* Gray, on islands with and without populations of the Polynesian rat, *Rattus exulans* (Peale). *Proceedings of the New Zealand Ecological Society 20*: 115-120.

Cuthbert, R.; Sommer, E.; Davis, L.S. 2000. Seasonal variation in the diet of stoats in a breeding colony of Hutton's shearwaters. *New Zealand Journal of Zoology 27*: 367-373.

Daniel, M.J. 1973. Seasonal diet of the ship rat (*Rattus r. rattus*) in lowland forest in New Zealand. *Proceedings of the New Zealand Ecological Society 20*: 21-30.

Daugherty, C.H.; Gibbs, G.W.; Hitchmough, R. 1993. Mega-island or micro-continent? New Zealand and its fauna. *Trends in Ecology & Evolution 8*: 437-442.

Daugherty, C.H.; Gibbs, G.W.; Towns, D.R.; Atkinson, I.A.E. 1990. The significance of the biological resources of New Zealand islands for ecological restoration. Conservation Sciences Publication (New Zealand), Department of Conservation, Wellington.

Daugherty, C.H.; Patterson, G.B.; Hitchmough, R.A. 1994. Taxonomic and conservation review of the New Zealand herpetofauna. *New Zealand Journal of Zoology 21*: 317-323.

Daugherty, C.H.; Towns, D.R. 1991. The cat's breakfast. *NewZealand science monthly*: 13-14.

Dawkins, R.; Krebs, J.R. 1979. Arms races between and within species. *Proceedings of the Royal Society of London. Series B. Biological Sciences 205*: 489-511.

Dial, B.E.; Fitzpatrick, L.C. 1981. The energetic costs of tail autotomy to reproduction in the lizard *Coleonyx brevis* (Sauria: Gekkonidae). *Oecologia 51*: 310-317.

Dial, B.E.; Fitzpatrick, L.C. 1984. Predator escape success in tailed versus tailless *Scincella lateralis* (Sauria: Scincidae). *Animal Behaviour 32*: 301-302.

Doughty, P.; Shine, R. 1998. Reproductive energy allocation and long-term energy stores in a viviparous lizard (*Eulamprus tympanum*). *Ecology 79*: 1073-1083.

Downes, S.; Shine, R. 2001. Why does tail loss increase a lizard's later vulnerability to snake predators? *Ecology 82*: 1293-1303.

Downes, S.J. 2002. Does responsiveness to predator scents affect lizard survivorship? *Behavioral Ecology and Sociobiology 52*: 38-42.

Dunham, A.E.; Miles, D.B.; Reznick, D.N. 1988. Life history patterns in squamate reptiles. *Biology of the Reptilia 16*: 441-522.

Dunlap, K.D.; Mathies, T. 1993. Effects of nymphal ticks and their interaction with malaria on the physiology of male fence lizards. *Copeia 1993*: 1045-1048.

Dunlap, K.D.; Schall, J.J. 1995. Hormonal alterations and reproductive inhibition in male fence lizards (*Sceloporus occidentalis*) infected with the malarial parasite *Plasmodium mexicanum*. *Physiological Zoology 68*: 608-621.

East, K.T.; East, M.R.; Daugherty, C.H. 1995. Ecological restoration and habitat relationships of reptiles on Stephens Island, New Zealand. *New Zealand Journal of Zoology 22*: 249-261.

Efford, M.; Spencer, N.J.; Thomas, B.W.; Mason, R.F. 1997. A population study of sympatric skinks on Lake Station, upper Buller Valley. *Proceedings of the Society for Research on Amphibians and Reptiles in New Zealand,* pp 323-332. New Zealand Journal of Zoology, Kaikoura.

Efford, M.G. 2014a. Package 'secr'. CRAN, Dunedin.

Efford, M.G. 2014b. secr: Spatially explicit capture-recapture models.CRAN.

Eisen, R.J. 2001. Absence of measurable malaria-induced mortality in western fence lizards (*Sceloporus occidentalis*) in nature: a 4-year study of annual and over-winter mortality. *Oecologia 127*: 586-589.

Elton, C.; Nicholson, M. 1942. The ten-year cycle in numbers of the lynx in Canada. *The Journal of Animal Ecology*: 215-244.

Endler, J.A. 1986. *Natural selection in the wild*. Princeton University Press, Princeton.

Ferguson, G.W.; Fox, S.F. 1984. Annual variation of survival advantage of large juvenile side-blotched lizards, *Uta stansburiana*: its causes and evolutionary significance. *Evolution*: 342-349.

Freeman, A.B. 1997. Comparative ecology of two *Oligosoma* skinks in coastal Canterbury: A contrast with Central Otago. *New Zealand Journal of Ecology 21*: 153-160.

Gibbon, J.W.; Scott, D.E.; Ryan, T.J.; Buhlmann, K.A.; Tuberville, T.D.; Metts, B.S.; Greene, J.L.; Mills, T.; Leiden, Y.; Poppy, S. 2000. The global decline of reptiles, déjà vu amphibians. *Bioscience 50*: 653-666.

Gibbons, J.; Stangel, P. 1999. Conserving amphibians and reptiles in the new millennium. *Proceedings of the Partners in Amphibian and Reptile Conservation (PARC) Conference*.

Gibbons, J.; Watkins, I. 1982. Behavior, ecology, and conservation of South Pacific banded iguanas, Brachylophus, including a newly discovered species. *Iguanas of the World: Their Behavior, Ecology and Conservation. Noyes Publications, Park Ridge, New Jersey, USA*: 418-441.

Gill, B.J. 1976. Aspects of the ecology, morphology, and taxonomy of two skinks (Reptilia: Lacertilia) in the coastal Manawatu area of New Zealand. *New Zealand Journal of Zoology 3*: 141-157.

Gleeson, T.T.; Hancock, T.V. 2002. Metabolic implications of a 'run now, pay later' strategy in lizards: an analysis of post-exercise oxygen consumption. *Comparative Biochemistry and Physiology-Part A: Molecular & Integrative Physiology 133*: 259-267.

Godfrey, S.S.; Moore, J.A.; Nelson, N.J.; Bull, C.M. 2010. Unravelling causality from correlations: revealing the impacts of endemic ectoparasites on a protected species (tuatara). *Parasitology 137*: 275-286.

Goin, J. 1992. Requiem or recovery. *Texas Parks Wildlife (August)*: 28-35.

GoldenSoftware. 2011. Grapher 9. Golden Software LLC, Golden.

Greaves, S.N.; Chapple, D.G.; Gleeson, D.M.; Daugherty, C.H.; Ritchie, P.A. 2007. Phylogeography of the spotted skink (*Oligosoma lineoocellatum*) and green skink (*O. chloronoton*) species complex (Lacertilia: Scincidae) in New Zealand reveals pre-Pleistocene divergence. *Molecular Phylogenetics and Evolution 45*: 729-739.

Greene, H.W. 1988. Antipredator mechanisms in reptiles. *Biology of the Reptilia 16*: 1-152.

Grigg, G.; Shine, R.; Ehmann, H. 1985. An overview of the ecological biogeography of the New Zealand lizards (Gekkonidae, Scincidae). *Biology of Australasian Frogs and reptiles*: 107.

Hamilton, W.D.; Zuk, M. 1982. Heritable true fitness and bright birds: a role for parasites? *Science: 218*: 384.

Hardy, G.S. 1977. The New Zealand Scincidae (Reptilia: Lacertilia); a taxonomic and zoogeographic study. *New Zealand Journal of Zoology 4*: 221-325.

Hare, K.M.; Hare, J.R.; Cree, A. 2010. Parasites, but not palpatation, are associated with pregnancy failure in a captive viviparous lizard. *Herpetological Conservation and Biology 5*: 563-570.

Hare, K.M.; Hoare, J.M.; Hitchmough, R.A. 2007. Investigating natural population dynamics of *Naultinus manukanus* to inform conservation management of New Zealand's cryptic diurnal geckos. *Journal of Herpetology 41*: 81-93.

Harwood, R. 1979. The effect of temperature on the digestive efficiency of three species of lizards, *Cnemidophorus tigris, Gerrhonotus multicarinatus* and *Sceloporus occidentalis*. *Comp. Biochem. Physiol. 63A 417*: 433.

Hay, J.M.; Sarre, S.D.; Lambert, D.M.; Allendorf, F.W.; Daugherty, C.H. 2010. Genetic diversity and taxonomy: a reassessment of species designation in tuatara (Sphenodon: Reptilia). *Conservation Genetics 11*: 1063-1081.

Head, M.L.; Keogh, J.S.; Doughty, P. 2002. Experimental evidence of an age-specific shift in chemical detection of predators in a lizard. *Journal of Chemical Ecology 28*: 541-554.

Heinen, J.T. 1994. An antiredator behavior of newly metamorphosed American toads (*Bufo-americanus-americanus*), and mechanisms of hunting by eastern garter snakes (*Thamnophis-sirtalis-sirtalis*). *Herpetologica 50*: 137-145.

Hicks, G.R.F.; McColl, H.P.; Meads, M.J.; Hardy, G.S.; Roser, R.J. 1975. An ecological reconnaissance of Korapuki Island, Mercury Islands. *Notornis 22*: 195-220.

Hitchmough, R.; Anderson, P.; Barr, B.; Monks, J.; Lettink, M.; Reardon, J.; Tocher, M.; Whitaker, T. 2013. Conservation status of New Zealand reptiles, 2012. *New Zealand Threat Classification Series*. Department of Conservation.

Hitchmough, R.; Hoare, J.; Jamieson, H.; Newman, D.; Tocher, M.; Anderson, P.; Lettink, M.; Whitaker, A. 2010. Conservation status of New Zealand reptiles, 2009. *New Zealand Journal of Zoology 37*: 203-224.

Hoare, J.M. 2006. Novel predators and naive prey: how introduced mammals shape behaviours and populations of New Zealand lizards. *Biology*. PhD. Victoria University of Wellington, Wellington.

Hoare, J.M.; Adams, L.K.; Bull, L.S.; Towns, D.R. 2007a. Attempting to manage complex predator-prey interactions fails to avert imminent extinction of a threatened New Zealand skink population. *The Journal of Wildlife Management 71*: 1576-1584.

Hoare, J.M.; O'Donnell, C.F.J.; Westbrooke, I.; Hodapp, D.; Lettink, M. 2009. Optimising the sampling of skinks using artificial retreats based on weather conditions and time of day. *Applied Herpetology 6*: 379-390.

Hoare, J.M.; Pledger, S.; Keall, S.N.; Nelson, J.; Mitchell, N.J.; Daugherty, C.H. 2006. Conservation implications of a long-term decline in body condition of the Brothers Island tuatara (*Sphenodon guntheri*). *Animal Conservation 9*: 456-462.

Hoare, J.M.; Pledger, S.; Nelson, N.J. 2007b. Chemical discrimination of food, conspecifics and predators by apparently visually-oriented diurnal geckos, *Naultinus manukanus*. *Herpetologica 63*: 184-192.

Hoare, J.M.; Pledger, S.; Nelson, N.J.; Daugherty, C.H. 2007c. Avoiding aliens: behavioural plasticity in habitat use enables large, nocturnal geckos to survive Pacific rat invasions. *Biological Conservation 136*: 510-519.

Holdaway, R.N. 1996. Arrival of rats in New Zealand. *Nature 384*: 225-226.

Hudson, P.J.; Dobson, A.P.; Newborn, D. 1998. Prevention of population cycles by parasite removal. *New Zealand Herpetology 282*: 2256.

Inkscape. 2014. Inkscape. Freedom Software Conservancy.

IUCN. 2015. The IUCN red list of threatened species. IUCN, Gland.

Iverson, J.B. 1978. The impact of feral cats and dogs on populations of the West Indian rock iguana, *Cyclura carinata*. *Biological Conservation 14*: 63-73.

Jaksić, F.M.; Greene, H.W. 1984. Empirical evidence of non-correlation between tail loss frequency and predation intensity on lizards. *Oikos*: 407-411.

Jennings, W.B.; Thompson, G.G. 1999. Territorial behavior in the Australian scincid lizard *Ctenotus fallens*. *Herpetologica*: 352-361.

Jewell, T. 2011. *A Photographic Guide to Reptiles and Amphibians in New Zealand. Revised Edition*. New Holland Publishers (NZ) Ltd., Auckland.

Jones, C.; Moss, K.; Sanders, M. 2005. Diet of hedgehogs (*Erinaceus europaeus*) in the upper Waitaki Basin, New Zealand: Implications for conservation. *New Zealand Journal of Ecology 29*: 29-35.

Kats, L.B.; Dill, L.M. 1998. The scent of death: Chemosensory assessment of predation risk by prey animals. *Ecoscience 5*: 361-394.

Kavaliers, M.; Choleris, E. 2001. Antipredator responses and defensive behavior: ecological and ethological approaches for the neurosciences. *Neuroscience & Biobehavioral Reviews 25*: 577-586.

Keall, S.N.; Nelson, N.J.; Phillpot, P.; Pledger, S.; Daugherty, C.H. 2001. Conservation in small places: reptiles on North Brother Island. *New Zealand Journal of Zoology 28*.

Kelehear, C.; Webb, J.K. 2006. Effects of tail autotomy on anti-predator behavior and locomotor performance in a nocturnal gecko. *Copeia 2006*: 803-809.

Kiesecker, J.M.; Blaustein, A.R. 1997. Population differences in responses of red-legged frogs (*Rana aurora*) to introduced bullfrogs. *Ecology 78*: 1752-1760.

King, C. 1983. The relationships between beech (*Nothofagus* sp.) seedfall and populations of mice (*Mus musculus*), and the demographic and dietary responses of stoats (*Mustela erminea*), in three New Zealand forests. *The Journal of Animal Ecology*: 141-166.

King, C. 2005. *The Handbook of New Zealand mammals*. Oxford University Press, Auckland.

Kleiber, C.; Zeileis, A. 2015. AER: Applied Econometrics with R. CRAN.

Kluge, A.G. 1967. Systematics, phylogeny, and zoogeography of the lizard genus *Diplodactylus* Gray (Gekkonidae). *Australian journal of zoology 15*: 1007-1108.

Klukowski, M.; Nelson, C.E. 2001. Ectoparasite loads in free-ranging northern fence lizards, *Sceloporus undulatus hyacinthinus*: effects of testosterone and sex. *Behavioral Ecology and Sociobiology 49*: 289-295.

Kotler, B.P.; Ayal, Y.; Subach, A. 1994. Effects of predatory risk and resource renewal on the timing of foraging activity in a gerbil community. *Oecologia 100*: 391-396.

Kotler, B.P.; Blaustein, L.; Brown, J.S. 1992. Predator facilitation: the combined effect of snakes and owls on the foraging behavior of gerbils. *Annales Zoologici Fennici,* pp 199-206.

Kotler, B.P.; Brown, J.S.; Hasson, O. 1991. Factors affecting gerbil foraging behaviour and rates of owl predation. *Ecology*: 2249-2260.

Kovacs, E.K.; Crowther, M.S.; Webb, J.K.; Dickman, C.R. 2012. Population and behavioural responses of native prey to alien predation. *Oecologia 168*: 947-957.

Laurie, W.; Brown, D. 1990. Population biology of marine iguanas (*Amblyrhynchus cristatus*). III. Factors affecting survival. *The Journal of Animal Ecology*: 545-568.

Laurila, A.; Järvi-Laturi, M.; Pakkasmaa, S.; Merilä, J. 2004. Temporal variation in predation risk: stage-dependency, graded responses and fitness costs in tadpole antipredator defences. *Oikos 107*: 90-99.

Le Galliard, J.; Ferriere, R.; Clobert, J. 2005. Juvenile growth and survival under dietary restriction: are males and females equal? *Oikos 111*: 368-376.

Lettink, M. 2007. Do counts of common skinks (*Oligosoma nigriplantare polychroma*) from artificail retreats provide an accurate index of population size? , p 22. Department of Conservation.

Lettink, M.; Norbury, G.; Cree, A.; Seddon, P.J.; Duncan, R.P.; Schwarz, C.J. 2010. Removal of introduced predators, but not artificial refuge supplementation, increases skink survival in coastal duneland. *Biological Conservation 143*: 72-77.

Lettink, M.; O'Donnell, C.F.; Hoare, J.M. 2011. Accuracy and precision of skink counts from artificial retreats. *New Zealand Journal of Ecology 35*: 236.

Liggins, L.; Chapple, D.G.; Daugherty, C.H.; Ritchie, P.A. 2008. A SINE of restricted gene flow across the Alpine Fault: phylogeography of the New Zealand common skink (*Oligosoma nigriplantare polychroma*). *Molecular Ecology 17*: 3668-3683.

Lima, S.L. 1998a. Nonlethal effects in the ecology of predator-prey interactions. *Bioscience 48*: 25-34.

Lima, S.L. 1998b. Stress and decision making under the risk of predation: recent developments from behavioral, reproductive, and ecological perspectives. *Advances in the Study of Behavior 27*: 215-290.

Lima, S.L.; Dill, L.M. 1990. Behavioral decisions made under the risk of predation - a review and prospectus. *Canadian Journal of Zoology-Revue Canadienne De Zoologie 68*: 619-640.

Lloyd, R.; Alford, R.A.; Schwarzkopf, L. 2009. Chemical discrimination among predators by lizards: Responses of three skink species to the odours of high- and low-threat varanid predators. *Austral Ecology 34*: 50-54.

Lu, H.L.; Ding, G.H.; Ding, P.; Ji, X.A. 2010. Tail Autotomy Plays No Important Role in Influencing Locomotor Performance and Anti-Predator Behavior in a Cursorial Gecko. *Ethology 116*: 627-634.

Maginnis, T.L. 2006. The costs of autotomy and regeneration in animals: a review and framework for future research. *Behavioral Ecology 17*: 857.

Magurran, A.E. 1999. The causes and consequences of geographic variation in antipredator behaviour. *Geographic Variation in Behavior. Perspectives on Evolutionary Mechanisms*: 139-163.

Main, A.R.; Bull, C.M. 2000. The impact of tick parasites on the behaviour of the lizard *Tiliqua rugosa*. *Oecologia 122*: 574-581.

Maiorana, V.C. 1977. Tail autotomy, functional conflicts and their resolution by a salamander. *Nature 265:* 533-535.

Martín, J.; López, P. 1999a. An experimental test of the costs of antipredatory refuge use in the wall lizard, *Podarcis muralis*. *Oikos 84*: 499-505.

Martín, J.; López, P. 1999b. When to come out from a refuge: risk-sensitive and state-dependent decisions in an alpine lizard. *Behavioral Ecology 10*: 487.

Martín, J.; Salvador, A. 1992. Tail loss consequences on habitat use by the Iberian rock lizard, *Lacerta monticola*. *Oikos*: 328-333.

Martín, J.; Salvador, A. 1993. Tail loss and foraging tactics of the Iberian rock-lizard, *Lacerta monticola*. *Oikos*: 318-324.

Massaro, M.; Starling-Windhof, A.; Briskie, J.V.; Martin, T.E. 2008. Introduced mammalian predators induce behavioural changes in parental care in an endemic New Zealand bird. *PloS one 3*: e2331.

Mazerolle, M. 2013. AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c). *R package version 1.32*. CRAN.

McCallum, J. 1986. Evidence of predation by kiore upon lizards from the Mokohinau Islands. *New Zealand Journal of Ecology 9*: 83-88.

Medel, R.G.; Jiménez, J.E.; Fox, S.F.; Jaksić, F.M. 1988. Experimental evidence that high population frequencies of lizard tail autotomy indicate inefficient predation. *Oikos*: 321-324.

Mella, V.S.A.; Cooper, C.E.; Davies, S. 2014. Behavioural responses of free-ranging western grey kangaroos (*Macropus fuliginosus*) to olfactory cues of historical and recently introduced predators. *Austral Ecology 39*: 115-121.

Meyer-Rochow, V. 1988. Behaviour of young tuatara (*Sphenodon punctatus*) in total darkness. *Tuatara 30*: 36-38.

Meyer-Rochow, V.B.; Teh, K. 1991. Visual predation by tuatara (*Sphenodon punctatus*) on the beach beetle (*Chaerodes trachyscelides*) as a selective force in the production of distinct colour morphs. *Tuatara 31*: 1-8.

Miller, L.R.; Gutzke, W.H.N. 1999. The role of the vomeronasal organ of crotalines (Reptilia : Serpentes : Viperidae) in predator detection. *Animal Behaviour 58*: 53-57.

Møller, A.; Christe, P.; Lux, E. 1999. Parasitism, host immune function, and sexual selection. *Quarterly Review of Biology 74*: 3-20.

Moulis, R. 1997. Predation by the imported fire ant (*Solenopsis invicta)* on loggerhead sea turtle (*Caretta caretta*) nests on Wassaw National Wildlife Refuge, Georgia. *Chelonian Conservation and Biology 2*: 433-436.

Navarro-Castilla, Á.; Barja, I. 2014. Antipredatory response and food intake in wood mice (*Apodemus sylvaticus*) under simulated predation risk by resident and novel carnivorous predators. *Ethology 120*: 90-98.

Neill, K.F. 1997. Restoration and the skinks of Matiu-Somes Island: the potential impacts of revegitation. p 78. Victoria University of Wellington.

Neilson, K.; Duganzich, D.; Goetz, B.; Waas, J.R. 2004. Improving search strategies for the cryptic New Zealand striped skink (*Oligosoma striatum*) through behavioural contrasts with the brown skink (*Oligosoma zelandicum*). *New Zealand Journal of Ecology 28*: 267-278.

Newman, D.G. 1986. Can tuatara and mice co-exist? The status of tuatara, *Sphenodon punctatus* (Reptilia: Rhynchocephalia), on the Whangamata Islands. *The offshore islands of northern New Zealand*: 179-186.

Newman, D.G. 1994. Effects of a mouse, *Mus musculus*, eradication programme and habitat change on lizard populations of Mana Island, New Zealand, with special reference to McGregor's skink, *Cyclodina macgregori*. *New Zealand Journal of Zoology 21*: 443-456.

Newman, D.G.; McFadden, I. 1990. Seasonal fluctuations of numbers, breeding, and food of kiore (*Rattus exulans*) on Lady Alice Island (hen and chickens group), with a consideration of

kiore: Tuatara (*Sphenodon punctatus*) relationships in New Zealand. *New Zealand Journal of Zoology 17*: 55-63.

Newman, D.G.; Watson, P. 1985. The contribution of radiography to the study of the reproductive ecology of the tuatara, *Sphenodon punctatus*. *In:* Grigg, G.; Shine, R.; Ehmann, H. (Editors), *Biology of Australasian Frogs and Reptiles*, pp 7-10. Surrey Beatty, Chipping Norton.

Niewiarowski, P.; Congdon, J.; Dunham, A.; Vitt, L.; Tinkle, D. 1997. Tales of lizard tails: effects of tail autotomy on subsequent survival and growth of free-ranging hatchling *Uta stansburiana*. *Canadian Journal of Zoology 75*: 542-548.

NIWA. 2014. CliFlo: NIWA's National Climate Database on the Web.

Nogales, M., Medina, F. M. 1996. A review of feral domestic cats (*Felis silvestris* f. catus) on the Canary Islands, with new data from the laurel forest of La Gomera. *Zeitschrift Fur Saugetierkunde 61*: 1-6.

Nogales, M.; RodrÍGuez-Luengo, J.L.; Marrero, P. 2006. Ecological effects and distribution of invasive non-native mammals on the Canary Islands. *Mammal Review 36*: 49-65.

Norbury, G. 2001. Conserving dryland lizards by reducing predator-mediated apparent competition and direct competition with introduced rabbits. *Journal of Applied Ecology*: 1350-1361.

Olesen, J.M.; Valido, A. 2003. Lizards as pollinators and seed dispersers: an island phenomenon. *Trends in Ecology & Evolution 18*: 177-181.

Oliver, W.R.B. 1955. *New Zealand Birds*. A H & A W Reed, Wellington.

Oppliger, A.; Celerier, M.; Clobert, J. 1996. Physiological and behaviour changes in common lizards parasitized by haemogregarines. *Parasitology 113*: 433-438.

Oppliger, A.; Clobert, J. 1997. Reduced tail regeneration in the common lizard, *Lacerta vivipara*, parasitized by blood parasites. *Functional Ecology 11*: 652-655.

Oppliger, A.; Clobert, J.; Lecomte, J.; Lorenzon, P.; Boudjemadi, K.; John-Alder, H. 1998. Environmental stress increases the prevalence and intensity of blood parasite infection in the common lizard *Lacerta vivipara*. *Ecology Letters 1*: 129-138.

Owen, K. 1997. Mokoia Island - the transforamtion of an island now home to endangered species., *New Zealand Conservation Management Group Annual Conference Porceedings*, pp 74-87.

Parrish, G.R.; Pierce, R.J. 1993. Reptiles of Motuopao Island, Northland, New Zealand. *Tane 34*: 53-58.

Parsons, M.H.; Blumstein, D.T. 2010. Feeling vulnerable? indirect risk cues differently influence how two marsupials respond to novel dingo urine. *Ethology 116*: 972-980.

Parsons, T.S. 1959. Nasal anatomy and the phylogeny of lizards. *Evolution 13*: 175-187.

Patterson, G. 1992. The ecology of a New Zealand grassland lizard guild. *Journal of the Royal Society of New Zealand 22*: 91-106.

Patterson, G.; Daugherty, C. 1990. Four new species and one new subspecies of skinks, genus *Leiolopisma* (Reptilia: Lacertilia: Scincidae) from New Zealand. *Journal of the Royal Society of New Zealand 20*: 65-84.

Peig, J.; Green, A.J. 2009. New perspectives for estimating body condition from mass/length data: the scaled mass index as an alternative method. *Oikos 118*: 1883-1891.

Peig, J.; Green, A.J. 2010. The paradigm of body condition: a critical reappraisal of current methods based on mass and length. *Functional Ecology 24: 6:* 1323-1332.

Pond, C. 1981. Storage. *Physiological ecology: an evolutionary approach to resource use. Sinauer Associates, Sunderland, Massachusetts, USA*: 190-210.

Pregill, G.K. 1986. Body size of insular lizards: a patern of Holocene dwarfism. *Evolution 40*: 997-1008.

Price, P.W. 1980. *Evolutionary biology of parasites*. Princeton Univ Pr, Princeton.

Punzo, F. 2008. Chemosensory recognition of the marbled whiptail lizard, *Aspidoscelis marmorata* (Squamata: Teiidae) to odors of sympatric lizards (*Crotophytus collaris*, *Coleonyx brevis*, *Eumeces obsoletus* and *Uta stansburiana*) that represent different predation risks. *Journal of Environmental Biology 29*: 57-61.

R Core Team. 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rahel, F.J.; Kolar, C.S. 1990. Trade-offs in the response of mayflies to low oxygen and fish predation. *Oecologia 84*: 39-44.

Ramcharan, C.W.; Sprules, W.G. 1991. Predator-induced behavioral defense and its ecological consequences for two calanoid copepods. *Oecologia 86*: 276-286.

Reardon, J.T.; Norbury, G. 2004. Ectoparasite and hemoparasite infection in a diverse temperate lizard assemblage at macraes flat, South Island, New Zealand. *Journal of Parasitology 90*: 1274-1278.

Reardon, J.T.; Whitmore, N.; Holmes, K.M.; Judd, L.M.; Hutcheon, A.D.; Norbury, G.; Mackenzie, D.I. 2012. Predator control allows critically endangered lizards to recover on mainland New Zealand. *New Zealand Journal of Ecology 36*: 141.

Ripley, B.; Venables, W. 2015. Feed-forward neural networks and multinomial log-linear models. CRAN.

Robb, J. 1986. *New Zealand amphibians and reptiles in colour*. Ralph Curtis Pub, Fort Myers.

Rodda, G. 1992. Loss of native reptiles associated with introductions of exotics in the Mariana Islands. *Pacific Science 46*: 399-400.

Rosell, F.; Holtan, L.B.; Thorsen, J.G.; Heggenes, J. 2013. Predator-naive brown trout (*Salmo trutta*) show antipredator behaviours to scent from an introduced piscivorous mammalian predator fed conspecifics. *Ethology 119*: 303-308.

Rufaut, C.G.; Gibbs, G.W. 2003. Response of a tree weta population (*Hemideina crassidens*) after eradication of the Polynesian rat from a New Zealand island. *Restoration Ecology 11*: 13–19.

Saarikko, J. 1992. Risk of predation and foraging activity in shrews. *Annales Zoologici Fennici*, pp 291-299.

Salo, P.; Korpimäki, E.; Banks, P.B.; Nordström, M.; Dickman, C.R. 2007. Alien predators are more dangerous than native predators to prey populations. *Proceedings of the Royal Society B: Biological Sciences 274*: 1237-1243.

Salvador, A.; Martin, J.; Lopez, P. 1995. Tail loss reduces home range size and access to females in male lizards, *Psammodromus algirus*. *Behavioral Ecology 6*: 382.

Salvador, A.; Martín, J.; López, P.; Veiga, J.P. 1996. Long-term effect of tail loss on home-range size and access to females in male lizards (*Psammodromus algirus*). *Copeia*: 208-209.

Schall, J.J. 1992. Parasite-mediated competition in Anolis lizards. *Oecologia 92*: 58-64.

Schall, J.J. 1996. Malarial parasites of lizards: Diversity and ecology. *Advances in Parasitology 37*: 255-333.

Schall, J.J.; Pianka, R.E. 1980. Evolution of escape behaviour diversity. *The American Naturalist 115*.

Schall, J.J.; Sarni, G.A. 1987. Malarial parasitism and the behavior of the lizard, *Sceloporus occidentalis*. *Copeia*: 84-93.

Schuster, J.P.; Schaub, G.A. 2001. Experimental Chagas disease: the influence of sex and psychoneuroimmunological factors. *Parasitology research 87*: 994-1000.

Schwenk, K. 1995. Of tounges and noses: chemoreception on lizards and snakes. *Tree 10*: 7-12.

Shine, R. 1980. "Costs" of reproduction in reptiles. *Oecologia 46*: 92-100.

Sih, A. 1987. Predators and prey lifestyles: An evolutionary and ecological overview. *In:* Kerfoot, W.C.; Sih, A. (Editors), *Predation: Direct and Indirect Impacts on Aquatic Communities.* . University Press of New England, Hanover.

Sih, A. 1992. Integrative approaches to the study of predation: general thoughts and a case study on sunfish and salamander larvae. *Annales Zoologici Fennici 29*: 183-198.

Sih, A.; Kats, L.B.; Moore, R.D. 1992. Effects of predatory sunfish on the density, drift, and refuge use of stream salamander larvae. *Ecology 73*: 1418-1430.

Simon, C.A.; Gravelle, K.; Bissinger, B.E.; Eiss, I.; Ruibal, R. 1981. The role of chemoreception in the iguanid lizard *Sceloporus jarrovi*. *Animal Behaviour 29*: 46-54.

Sinclair, A.; Pech, R.P.; Dickman, C.; Hik, D.; Mahon, P.; Newsome, A. 1998. Predicting effects of predation on conservation of endangered prey. *Conservation Biology 12*: 564-575.

Sinervo, B.; Hedges, R.; Adolph, S.C. 1991. Decreased sprint speed as a cost of reproduction in the lizard Sceloporus occidentalis: variation among populations. *Journal of Experimental Biology 155*: 323-336.

Smallridge, C.J., and Bull, C. M. . 2000. Prevalence and intensity of the blood parasite *Hemolivia mariae* in a field population of the skink *Tiquila rugosa*. *Parasitology research 86*: 655–660.

Smyth, M. 1974. Changes in the fat scores of the skinks *Morethia boulengeri* and *Hemiergis peronii* (Lacertilia). *Australian journal of zoology 22*: 135-145.

Sorci, G.; Clobert, J. 1995. Effects of maternal parasite load on offspring life-history traits in the common lizard (*Lacerta vivipara*). *Journal of Evolutionary Biology 8*: 711-723.

Souter, N.J.; Bull, M., C; Hutchinson, M.N. 2004. Adding burrows to enhance a population of the endangered pygmy blue tongue lizard, *Tiliqua adelaidensis*. *Biological Conservation 116*: 403-408.

Spencer, N.J.; Thomas, B.W.; Mason, R.F.; Dugdale, J.S. 1998. Diet and life history variation in the sympatric lizards *Oligosoma nigriplantare polychroma* and *Oligosoma lineoocellatum*. *New Zealand Journal of Zoology 25*: 457-463.

Spitzen-van der Sluijs, A.; Spitzen, J.; Houston, D.; Stumpel, A.H. 2009. Skink predation by hedgehogs at Macraes Flat, Otago, New Zealand. *New Zealand Journal of Ecology 33*: 205-207.

SPSS. 2007. SPSS for Windows. SPSS Inc., Chicago.

Stapley, J. 2003. Differential avoidance of snake odours by a lizard: Evidence for prioritized avoidance based on risk. *Ethology 109*: 785-796.

Stephens, C. 2004. Plant succession, ecological restoration and the skinks of Stephens Island / Takapourewa. *Biology*, p 122. Msc.Victoria University of Wellington, Wellington.

Strauss, S.Y.; Lau, J.A.; Carroll, S.P. 2006. Evolutionary responses of natives to introduced species: what do introductions tell us about natural communities? *Ecology Letters 9*: 357-374.

Taylor, R.H.; Thomas, B.W. 1993. Rats eradicated from rugged Breaksea island (170 ha), Fiordland, New Zealand. *Biological Conservation 65*: 191-198.

Thomas, B.W.; Whitaker, A.H. 1995. Translocation of the Fiordland skink *Leiolopisma acrinasum* to Hawea Island, Breaksea Sound, Fiordland, New Zealand. *Reintroduction biology ofAustralian and New Zealand fauna. Surrey Beatty, Chipping Norton [Aust.]*: 91-95.

Tocher, M. 2006. Survival of Grand and Otago skinks following predator control. *Journal of Wildlife Management 70*: 31-42.

Towns, D.; Elliott, G. 1996. Effects of habitat structure on distribution and abundance of lizards at Pukerua Bay, Wellington, New Zealand. *New Zealand Journal of Ecology 20*: 191-206.

Towns, D.R. 1991. Response of lizard assemblages in the Mercury Islands, New Zealand, to removal of an introduced rodent: The kiore (*Rattus exulans*). *Journal of the Royal Society of New Zealand 21*: 119-136.

Towns, D.R. 1994. The role of ecological restoration in the conservation of Whitaker's skink (*Cyclodina whitakeri*), a rare New Zealand lizard (Lacertilia: Scincidae). *New Zealand Journal of Zoology 21*: 457-471.

Towns, D.R. 1996. Changes in habitat use by lizards on a New Zealand island following removal of the introduced Pacific rat *Rattus exulans*. *Pacific conservation biology 2*: 286-292.

Towns, D.R. 2002. Interactions between geckos, honeydew scale insects and host plants revealed on islands in northern New Zealand, following eradication of introduced rats and rabbits. *In:* Veitch, C.R.; Clout, M.N. (Editors), *Turning the tide: the eradication of invasive species*, p 329. IUCN, Gland.

Towns, D.R. 2009. Eradications as reverse invasions: lessons from Pacific rat (*Rattus exulans*) removals on New Zealand islands. *Biological Invasions 11*: 1719-1733.

Towns, D.R.; Atkinson, I.A.E.; Daugherty, C.H. 2006. Have the harmful effects of introduced rats on islands been exaggerated? *Biological Invasions 8*: 863-891.

Towns, D.R.; Daugherty, C.H. 1994. Patterns of range contractions and extinctions following human colonisation. *New Zealand Journal of Zoology 21*: 325-339.

Towns, D.R.; Daugherty, C.H.; Cree, A. 2001. Raising the prospects for a forgotten fauna: a review of 10 years of conservation effort for New Zealand reptiles. *Biological Conservation 99*: 3-16.

Towns, D.R.; Ferreira, S.M. 2001. Conservation of New Zealand lizards (Lacertilia: Scincidae) by translocation of small populations. *Biological Conservation 98*: 211-222.

Towns, D.R.; Neilson, K.A.; Whitaker, A.H. 2002. North Island *Oligosoma* spp. skink recovery plan 2002-2012. *New Zealand Department of Conservation Threatened Species Recovery Plan 48*.

Towns, D.R.; Simberloff, D.; Atkinson, I.A.E. 1997. Restoration of New Zealand islands: redressing the effects of introduced species. *Pacific conservation biology 3*: 99-124.

Troncoso-Palacios, J.; Labra, A. 2012. Is the exploratory behavior of *Liolaemus nitidus* modulated by sex? *Acta Herpetologica 7*: 69-80.

Turner, F.B.; Jennrich, R.I.; Weintraub, J.D. 1969. Home ranges and body size of lizards. *Ecology*: 1076-1081.

Tyrrell, C.L.; Cree, A.; Towns, D.R. 2000. Variation in reproduction and condition of northern tuatara (*Sphenodon punctatus punctatus*) in the presence and absence of kiore. *Science for conservation 153*: 42.

Van Damme, R.; Quick, K. 2001. Use of predator chemical cues by three species of lacertid lizards (*Lacerta bedriagae, Podarcis tiliguerta,* and *Podarcis sicula*). *Journal of Herpetology 35*: 27-36.

Van Valen, L. 1973. A new evolutionary law. *Evolutionary theory 1*: 1-30.

Vandamme, R.; Bauwens, D.; Thoen, C.; Vanderstighelen, D.; Verheyen, R.F. 1995. Responses of Naive Lizards to Predator Chemical Cues. *Journal of Herpetology 29*: 38-43.

Vinson, J.; Vinson, J. 1969. The saurian fauna of the Mascarene Islands. *Mauritius Inst. Bull. 6*: 203-320.

Vinson, J.a.Vinson, J. 1969. The saurian fauna of the Mascarene Islands. *Mauritius Inst. Bull. 6*: 203-320.

Vitt, L.J.; Congdon, J.D.; Dickson, N.A. 1977. Adaptive strategies and energetics of tail autonomy in lizards. *Ecology*: 326-337.

Vitt, L.J.; Cooper Jr, W.E. 1986. Tail loss, tail color, and predator escape in Eumeces (Lacertilia: Scincidae): age-specific differences in costs and benefits. *Canadian Journal of Zoology 64*: 583-592.

Vitt, L.J.; Pianka, E.R. 2005. Deep history impacts present-day ecology and biodiversity. *Proceedings of the National Academy of Sciences 102*: 7877.

Warnes, G.; Bolker, B.; Gorjanc, G.; Grothendieck, G.; Korosec, A.; Lumley, T.; MacQueen, D.; Magnusson, A.; Rogers, J. 2013. gdata: Various R programming tools for data manipulation. *R package version 2.13.2*. CRAN.

Weber, A.; Van Noordwijk, A. 2002. Swimming behaviour of Daphnia clones: differentiation through predator infochemicals. *Journal of Plankton Research 24*: 1335-1348.

Whitaker, A.H. 1967. Baiting pitfall traps for small lizards. *Herpetologica 23*: 309-310.

Whitaker, A.H. 1968. The lizards of the Poor Knights Islands, New Zealand. *New Zealand journal of science 11*: 623-651.

Whitaker, A.H. 1973. Lizard populations on islands with and without Polynesian rats, Rattus exulans (Peale). *Proceedings of the New Zealand Ecological Society 20*: 121-130.

Whitaker, A.H. 1978. The effects of rodents on reptiles and amphibians. *The ecology and control of rodents in New Zealand nature reserves*: 75-86.

Whitaker, A.H. 1987. The roles of lizards in New Zealand plant reproductive strategies. *New Zealand journal of botany 25*: 315-328.

Whitaker, T. 2000. *Lizards of Nelson and Marlborough A Feild Key*. Department of Conservation, Nelson.

Wilmshurst, J.M.; Higham, T.F. 2004. Using rat-gnawed seeds to independently date the arrival of Pacific rats and humans in New Zealand. *The Holocene 14*: 801-806.

Wilson, D.J.; Lee, W.G. 2010. Primary and secondary resource pulses in an alpine ecosystem: snow tussock grass (*Chionochloa* spp.) flowering and house mouse (*Mus musculus*) populations in New Zealand. *Wildlife Research 37*: 89-103.

Wilson, D.J., Mulvey R. L., Clark R. D. 2007. Sampling skinks and geckos in artifcial cover objects in a dry mixed grassland-shrubland with mammalian predator control. *New Zealand Journal of Ecology 31*: 169-185.

Wilson, K.J. 2004. *Flight of the huia: ecology and conservation of New Zealand's frogs, reptiles, birds and mammals*. Canterbury University Press, Christchurch.

Wilson, R.S.; Booth, D.T. 1998. Effect of tail loss on reproductive output and its ecological significance in the skink *Eulamprus quoyii*. *Journal of Herpetology 32*: 128-131.

Worthy, T.H. 1987a. Osteological observations on the larger species of the skink *Cyclodina* and the subfossil occurrence of these and the gecko *Hoplodactylus duvaucelii* in the North Island, New Zealand. *New Zealand Journal of Zoology 14*: 219-229.

Worthy, T.H. 1987b. Osteology of Leiopelma (Amphibia: Leiopelmatidae) and descriptions of three new subfossil Leiopelma species. *Journal of the Royal Society of New Zealand 17*: 201-251.

Worthy, T.H. 1987c. Palaeoecological information concerning members of the frog genus Leiopelma: Leiopelmatidae in New Zealand. *Journal of the Royal Society of New Zealand 17*: 409-420.

Worthy, T.H.; Holdaway, R.N. 2002. *The lost world of the moa: prehistoric life of New Zealand*. Indiana Univ Pr., Bloomington.

Worthy, T.H.; Tennyson, A.J.; Archer, M.; Musser, A.M.; Hand, S.J.; Jones, C.; Douglas, B.J.; McNamara, J.A.; Beck, R.M. 2006. Miocene mammal reveals a Mesozoic ghost lineage on insular New Zealand, southwest Pacific. *Proceedings of the National Academy of Sciences 103*: 19419-19423.

Wozniak, E.J.; Kazacos, K.R.; Telford, S.R. 1996. Characterization of the clinical and anatomical pathological changes associated with *Hepatozoon mocassini* infections in unnatural reptilian hosts. *International journal for parasitology 26*: 141-146.